

**LIMNOLOGICAL PERSPECTIVES ON
STOCK AND RECRUITMENT
FOR EGEGIK AND UGASHIK RIVER
SOCKEYE SALMON**

by

J. A. Edmundson and G. L. Todd

REGIONAL INFORMATION REPORT¹ No. 2A00-33

**Alaska Department of Fish and Game
Division of Commercial Fisheries
333 Raspberry Road
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November 2000

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ABSTRACT

Edmundson, J. A. and G. L. Todd. 2000. Limnological perspectives on stock and recruitment for Egegik and Ugashik River sockeye salmon. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report No. 2A00-33:90pp.

Sockeye salmon (*Oncorhynchus nerka*) production of the Egegik River and nearby Ugashik River systems (Bristol Bay) showed a dramatic increase beginning in the late 1970s. However, poor sockeye returns to Bristol Bay in 1996 and 1997 prompted initiation of limnological studies of Becharof Lake of the Egegik River system and Upper and Lower Ugashik lakes in the Ugashik River system to determine if freshwater aspects of sockeye salmon were limiting production. We examined recent limnological data in conjunction with historical spawner-recruit (S-R) and smolt information to characterize the rearing capacity of Becharof and Ugashik lakes and to assess the current escapement goals. For both systems, Ricker stock-recruit analysis failed to describe adult sockeye production patterns. However, adult recruits were roughly proportional to the size of spawning stock. Although, adult recruits were positively related to the total number of smolts, adult recruits-per-smolt were inversely related to total smolt output. Yet, there was no functional relationship between the number of spawners and subsequent smolt production. While escapements in these two systems have increased in recent years, smolt production and the number of smolts-per-spawner declined. It has been suggested that the large variability and decline in smolt production resulted in part from either a lack of suitable spawning area, insufficient forage (zooplankton) for rearing juveniles, temperature shifts, or a build-up of predators (piscivory effects). In both lakes, spawner densities were relatively low, but average zooplankton densities and biomass were high compared to other sockeye nursery lakes. In addition, average smolt sizes have been fairly large and consistent over the past two decades. Smolt size was also unrelated to the total number of smolts suggesting little density-dependent growth relative to the forage base (zooplankton) was occurring. Although terrestrial air temperatures in the Bristol Bay region have increased over the past two decades, smolt size, proportion of age 1 smolts, and adult recruits-per-spawner were uncorrelated with the summer monthly air temperature anomalies. There appeared to be a weak 4-5 year cycle associated with smolt abundances by brood year in Becharof Lake, suggesting a possible predator effect; however, such a pattern was not evident for Ugashik smolt. Considering spawning area limitations, food supply (zooplankton), temperature, and predators, we believe it is the lack of suitable spawning area that limits sockeye production in the Egegik and Ugashik systems. Based on examination of temporal trends in S-R data, Markov probability tables, and limnological characteristics we developed estimates of optimum escapements for the two systems. Integration of limnological data with S-R information is useful in assessing escapement goals and helps disentangle the total mortality of sockeye salmon across the freshwater and marine components.

INTRODUCTION

The Egegik and Ugashik River systems are important producers of sockeye salmon (*Oncorhynchus nerka*) in the Bristol Bay region of southwest Alaska. Annual runs for the two systems combined exceed 20 million in some years (Cross et al. 1997). As such, commercial catches of sockeye salmon are of great economic value to the region. Like many salmon stocks, there is a large variability in magnitude of these runs that is attributed in part to natural fluctuations in ocean and freshwater survival. Commercial catches of these stocks generally increased from the late 1970s to the early 1990s; however, total returns and system productivity, as indexed by recruits-per-spawner (R/S), for the Egegik and Ugashik stocks have declined in recent years (Cross et al. 1997; Mathisen et al. 1998). Although the specific cause(s) is unknown, this has led some investigators to speculate that much of the observed variability in sockeye production for these stocks is tied to changes in spawning or rearing conditions in their primary nursery lakes: Becharof Lake of the Egegik River system and Upper and Lower Ugashik lakes of the Ugashik River system.

At least four explanations or hypotheses have emerged surrounding the variability in freshwater sockeye production for the Egegik and Ugashik sockeye salmon stocks. First, although effective spawning areas were not quantified for either system, Burgner et al. (1969) pointed out that both systems had lower sockeye escapement per unit lake area compared with several other systems in Bristol Bay and southwest Alaska. There is also some consensus among Alaska Department of Fish and Game (ADF&G) fisheries staff that both systems are probably spawning area limited, though this has not been formally documented. Second, Mathisen et al. (1998) suggested that the observed increase in sockeye salmon production for Egegik and Ugashik sockeye stocks that occurred throughout the 1970s was attributed to warmer water temperatures and greater primary productivity in their nursery lakes. Third, there is some evidence, at least in Becharof Lake, for brood-year interaction; i.e., sockeye fry of adjacent year classes may compete for limited food (zooplankton) resources (Martin and Lloyd 1996). Fourth, it has been suggested that juvenile sockeye production in Becharof and Ugashik lakes is to a large extent under predator (piscivore) control (Mathisen 1997; Mathisen and Sands 1999). Whatever the cause(s), determination of escapement levels that maximize smolt output and subsequent adult returns is crucial to efficient management of these stocks.

Several investigators have analyzed S-R relationships for the Egegik and Ugashik sockeye salmon to assess harvest strategies and estimate optimum escapement levels (Fried 1984; Cross 1991; Cross et al. 1997). However, standard S-R methods (e.g., linear transformation of a compensatory Ricker model [Ricker 1975]) have failed to adequately describe or characterize sockeye production patterns in these two stocks, despite reliable measures of stock and recruitment and a broad range (order of magnitude) of spawning stock sizes (Cross et al. 1997). Nonetheless, stock and recruitment dynamics can be affected by habitat or environmental changes that manifest as a de-coupling between the size of parental stock and adult recruits (Hilborn and Walters 1992; Hayes et al. 1996). Thus, there has been some uncertainty in determining the optimal escapement levels for

the Egegik and Ugashik sockeye salmon stocks. That is, escapements below the optimum could result in reduced yield or perhaps an exhaustion of essential marine nutrients (Kline et al. 1997). On the other hand, escapements above the optimum might be wasting harvestable surplus. If escapements are excessively high, particularly for consecutive years, this can lead to a long-term decline in sockeye productivity through effects of overgrazing on the forage base (zooplankton) by large fry recruitments (Kyle et al. 1988). Overescapements may also induce behavioral changes in zooplankton populations that result in some spatial (vertical) mismatch between prey availability and sockeye juveniles as suggested by Schmidt et al. (1996).

Currently, Egegik and Ugashik River sockeye salmon stocks are managed with a biological escapement goal (BEG). For the Egegik River the escapement point goal is 1.1 million with a range of 0.8 million to 1.4 million and for Ugashik River the BEG point goal is 0.85 million with a range of 0.5 million to 1.2 million (Fair 2000). The BEGs are the estimated number of spawners to produce maximum sustained yield (MSY) based on a combination of tabular summaries of the S-R data and the relationships between number of spawners and various smolt population characteristics. MSY is also based on Ricker models. Brood tables have been developed from adult escapement, harvest data, and age composition for both stocks beginning in 1956. Estimates of smolt abundance based on riverine sonar counts, as well as information on smolt size and age composition are available for Egegik and Ugashik rivers beginning with brood years 1978 and 1980, respectively (Crawford 2000).

Prompted in part by the lower than expected production of sockeye smolt for the Egegik and Ugashik systems in recent years and the poor sockeye runs to most Bristol Bay systems that occurred in 1996 and 1997, ADF&G in cooperation with the U.S. Fish and Wildlife Service (USFWS) and Lake and Peninsula Borough (LPB) initiated limnological studies of Becharof and Ugashik lakes. The purpose of this project was to evaluate the rearing capacity relative to juvenile sockeye salmon production and to assess the usefulness of complementing stock and recruitment data with limnological information to assess escapement goals. The utility of integrating habitat (limnological) information with S-R data, which resulted in a recommendation for a revised escapement goal (BEG), was nicely demonstrated for the Karluk Lake sockeye salmon (Schmidt et al. 1998). Unfortunately, unlike the Karluk Lake study, our time series of limnological data is very short, only three years (1997-1999). Nonetheless, our studies are the first to consistently examine major trophic levels (i.e., phytoplankton-zooplankton-juvenile sockeye-adult sockeye) as well as measurements of salient nutrient (e.g., phosphorus and nitrogen) and physical variables (e.g., light and temperature) in Becharof and Ugashik lakes.

Objectives

Our specific objectives in this report were three-fold: (1) characterize the freshwater rearing habitat of the nursery lakes and focus on temporal (seasonal and inter-annual) and spatial variability, (2) utilize pertinent limnological data to evaluate the various hypotheses put forth concerning freshwater production of sockeye salmon, and (3)

provide an analysis of limnological and fisheries data to determine optimum escapement goals for the Egegik and Ugashik sockeye stocks.

Description of Study Lakes

The Egegik and Ugashik River systems are located on the east side of Bristol Bay near the base of the Alaska Peninsula (Figure 1). Becharof Lake drains via the Egegik River and the Ugashik lakes drain via Ugashik River, both systems flow into Bristol Bay. The lakes are situated at an elevation less than 15 m. Because of their close proximity to the Gulf of Alaska, they experience a maritime climate with frequent and persistent winds. These winds exert a strong influence on mixing patterns and thermal structure such that the lakes have relatively long ice-free periods compared to more interior lakes (LaPerriere 1997). Since 1979, the mean duration of ice cover was only 72 days for Becharof Lake and 84 days for Ugashik lakes (Mathisen et al. 1998), but anecdotal evidence indicates that in some years the lakes may not freeze over at all. From a limnological perspective, neither system has been studied in any great detail. Prior to 1996, the only morphometric information (i.e., area, elevation) available for Becharof and Ugashik lakes was from U.S. Geological Survey topographic maps. Recently, Mathisen (1996) charted the bathymetry of each lake. Subsequently, Spafard and Edmundson (2000) reported the morphometrics. Becharof Lake (57° 53'N, 156° 30'W) has a surface area of 1,142.7 km² making it the 3rd largest freshwater lake in the United States outside of the Laurentian Great Lakes. It has a mean depth of 56.7 m and a maximum depth of 181 m (Figure 2). In addition to the east and west main basins that compose about 90% of the total lake surface area, there are two smaller, shallower basins identified as Island Arm and Ruth Arm that are thought to support large numbers of beach spawning salmon. Becharof Lake is notable for its unusual geologic feature known as the Gas Rocks along the south shore where a large fault along the lake bottom visibly degasses carbon dioxide into the water column (Symonds et al. 1997). Trace metals analysis of the surrounding waters revealed elevated concentrations of boron and lithium, which indicated geothermic activity (Symonds et al. 1997). Nearby Ugashik Lake has two distinct basins (usually referred to as Upper and Lower Ugashik lakes), the upper basin having its longitudinal axis perpendicular to that of the lower basin. Upper Ugashik Lake (57° 40'N, 156° 40'W) has a surface area of 199.4 km², a mean depth of 28.6 m, and a maximum depth of approximately 150 m (Figure 3). Lower Ugashik Lake has a surface area of 182.3 km², a mean depth of 35.7 m, and a maximum depth of 120 m (Figure 4). An unusual feature of the Ugashik lakes is that previous synoptic surveys revealed a conspicuous absence of cladoceran zooplankton (water fleas) populations (Mathisen et al. 1998), an important group of zooplankton well represented numerically in most other clear water lakes with or without planktivorous fish.

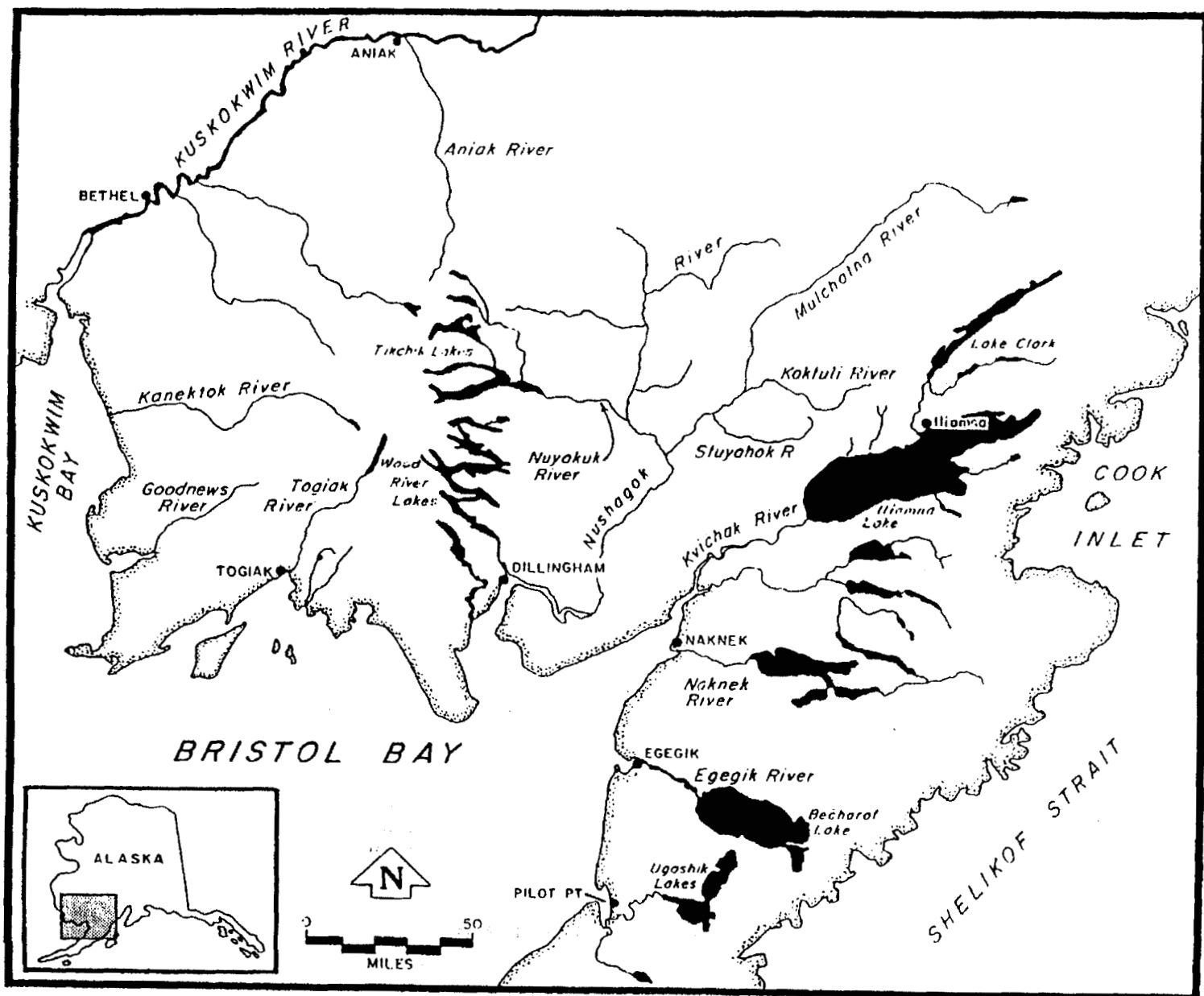


Figure 1. Geographic location of Becharof and Ugashik lakes.

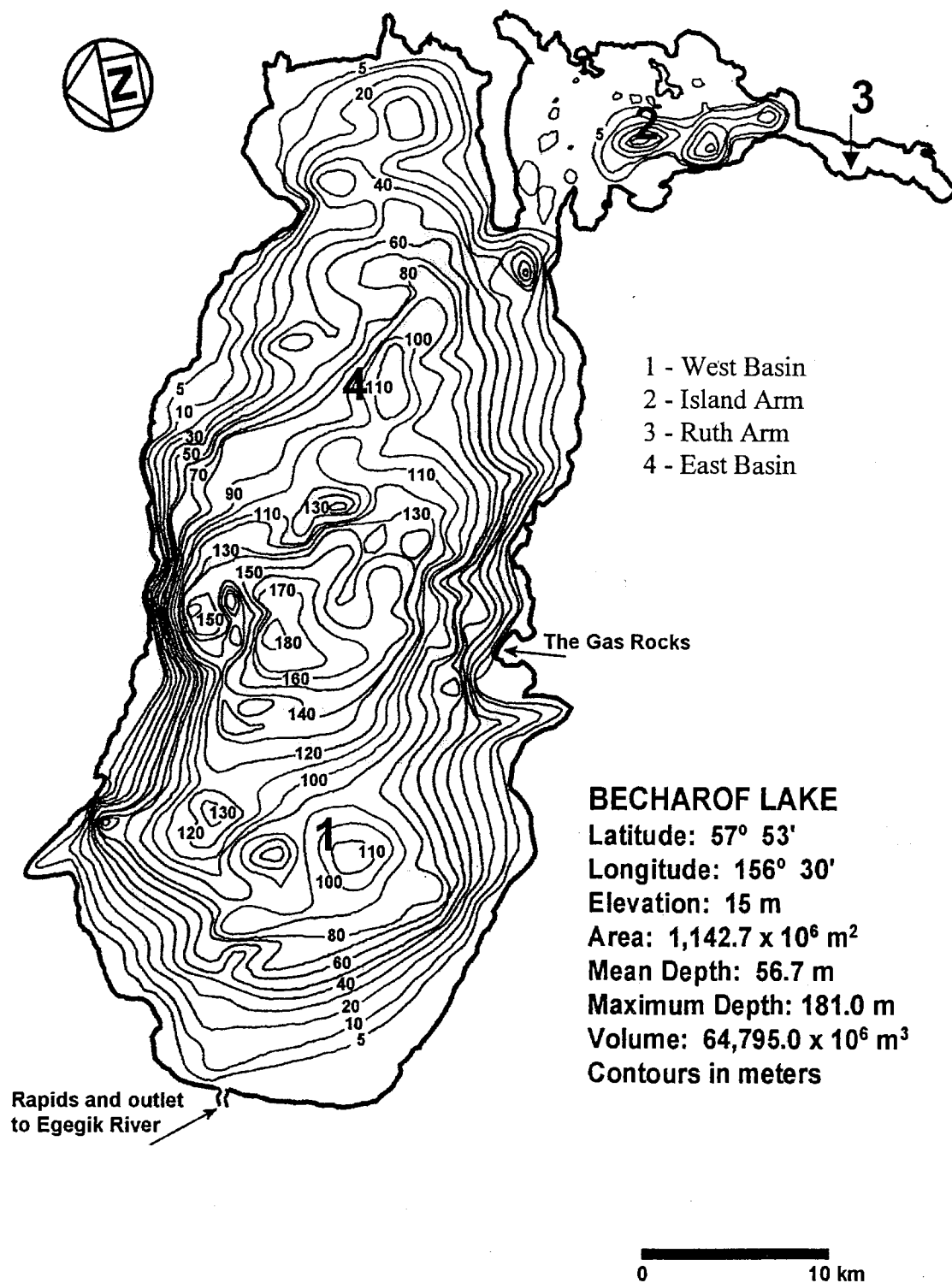


Figure 2. Bathymetric map of Becharof Lake showing locations of the limnology sampling stations (1-4). Map modified from Mathisen (1996).

UPPER UGASHIK LAKE

Latitude: 57° 40'

Longitude: 156° 40'

Elevation: 3 m

Area: $199.4 \times 10^6 \text{ m}^2$

Mean Depth: 28.6 m

Maximum Depth: 150.0 m

Volume: $5,704.1 \times 10^6 \text{ m}^3$

Contours in meters

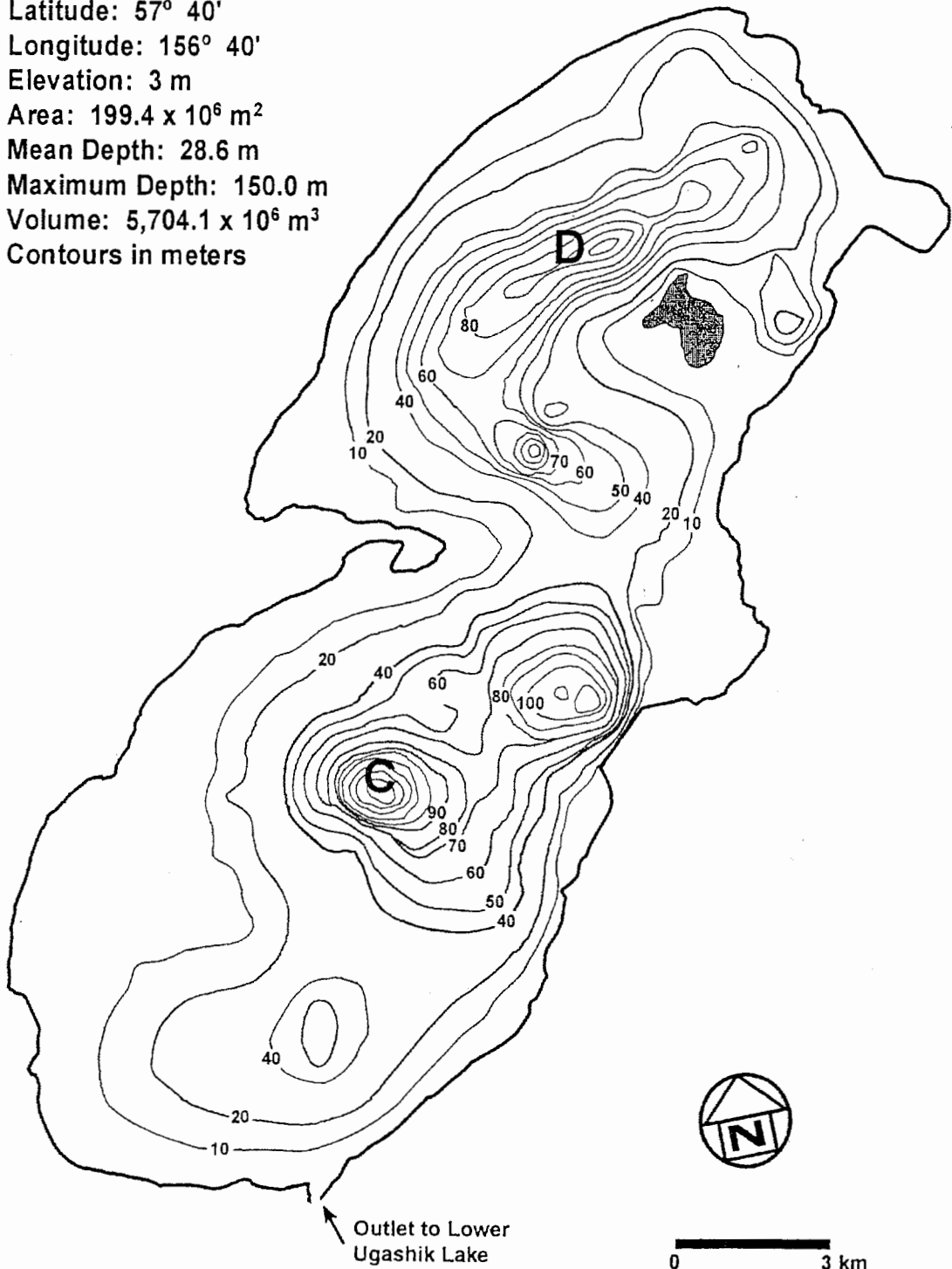
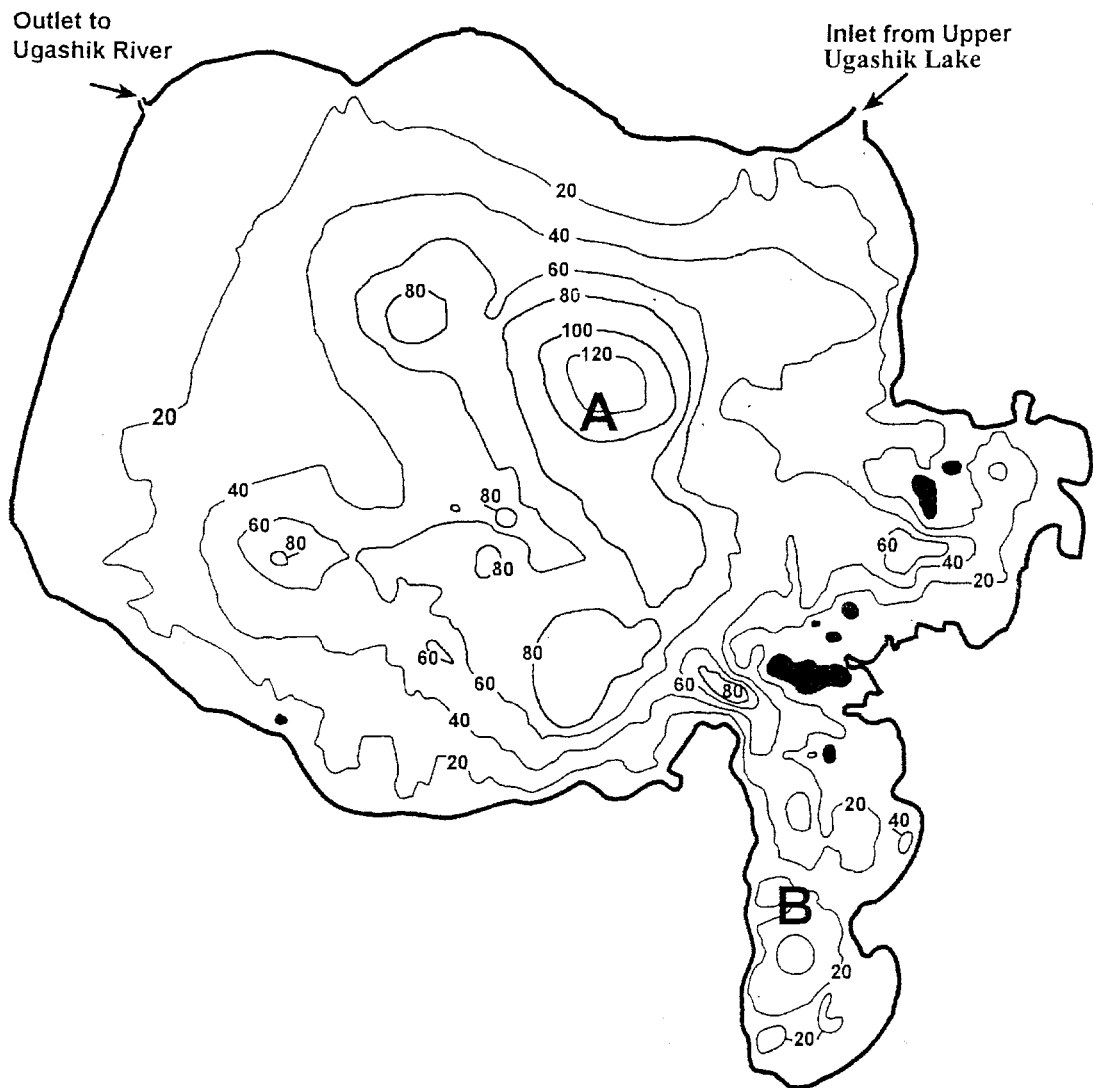


Figure 3. Bathymetric map of Upper Ugashik Lake showing locations of the limnology sampling stations (C-D). Map modified from Mathisen (1996).



LOWER UGASHIK LAKE

Latitude: 57° 30'

Longitude: 157° 08'

Elevation: 3 m

Area: $182.3 \times 10^6 \text{ m}^2$

Mean Depth: 35.7 m

Maximum Depth: 120.0 m

Volume: $6,484.0 \times 10^6 \text{ m}^3$

Contours in meters



0 3 km

Figure 4. Bathymetric map of Lower Ugashik Lake showing locations of the limnology sampling stations (A-B). Map modified from Mathisen (1996).

METHODS

Sockeye Salmon Data

Total abundance of sockeye salmon spawners and corresponding adult data for the Egegik and Ugashik runs were available from brood year 1956 to 1995. Since a classic Ricker model does not adequately describe the stock-recruitment (S-R) data for the Egegik and Ugashik sockeye (Cross et al. 1997), we considered a density-independent model. We also examined S-R data by using Markov transition probability tables as described by Hilborn and Walters (1992). We developed two tables using discrete escapement intervals of 300,000 fish, which were offset from each other by 150,000 fish. We computed mean spawner abundance, adult recruits, and yield for each interval. We also examined the tabular data graphically. Data on smolt production was obtained from Crawford (2000). Smolt abundance and size at age data for the Egegik River by brood year were available from 1978 to 1996. For Ugashik River sockeye, smolt data were available for brood years 1981 to 1996, with two exceptions: the smolt enumeration project was not conducted in 1992, so smolt estimates are incomplete for brood years 1989 and 1990.

Limnological Data

The data reported here were obtained from a three-year sampling program that began in July 1997 and ended in October 1999. At Becharof Lake, we sampled four locations: the main Basin (Station 1), Island Arm (Station 2), Ruth Arm (Station 3), and East Basin (Station 4). In 1997, sampling was conducted approximately once per month from July to October and in 1998 and 1999 we sampled once per month from June to September. The Ugashik lakes system was also sampled from four sites: two in the lower basin (Stations A and B) and two in the upper basin (Stations C and D). In 1997, sampling was carried out about once per month from July to September, but during 1998 and 1999 the lake was sampled once per month in June, July, and September. All sampling sites were selected to represent the lake's major basins or bays and were located by geographical position system and echo sounder. Approximate locations of the limnological sampling sites are shown on the respective bathymetric maps (Figures 2-4).

We measured underwater irradiance with an International Light submarine photometer equipped with a cosine corrected sensor. Vertical light extinction coefficients (K_d), the rate (m^{-1}) of underwater light decay, and euphotic zone depth (EZD), the estimated maximum depth of net primary production, were calculated according to standard methods (e.g., see Wetzel and Likens 1991). The EZD is defined here as the depth to which 1% of the subsurface light penetrates. Water clarity was measured with a Secchi disk (SD). Vertical profiles of temperature were measured from the surface to 50 m (maximum depth of submersible sensor) using a YSI model oxygen analyzer equipped with a thermistor.

We used an 8-L Van Dorn bottle to collect all water samples. Water was collected from the 1 m depth from both lakes at all sites. Deeper water samples were also collected from 50 m at each site, except at Island Arm (Station 2; Becharof Lake), which was sampled at either 40 m or 50 m and at Ruth Arm (Station 3; Becharof Lake), which was sampled at variable depths between 10 m and 15 m. Water for dissolved nutrients and color determination were filtered through Whatman GFF glass-fiber filters that were rinsed with deionized water before filtration. We stored filtered water in acid washed and deionized water rinsed polyethylene (poly) bottles until analysis. Unfiltered water samples were stored refrigerated for analysis of general water chemistry parameters. Separate aliquots of unfiltered water were stored frozen in clean polybottles for determination of total phosphorus and Kjeldahl nitrogen. All chemical and biological analyses were conducted by ADF&G limnology laboratory, Soldotna.

In the laboratory, conductivity (temperature compensated to 25° C) was measured using a YSI conductance meter, and pH was measured with an Orion model 420A pH meter. Alkalinity was determined by acid (0.02 N H₂SO₄) titration to pH 4.5 units. Turbidity, expressed as nephelometric turbidity units (NTU) was measured with a HF model 00B meter, and color was determined on a filtered (GFF) sample by measuring the spectrophotometric absorbance at 400 nm and converting to equivalent platinum cobalt (Pt) units. Calcium and magnesium were determined from separate EDTA (0.01 N) titrations, and total iron was analyzed by reduction of ferric iron with hydroxylamine during hydrochloric acid digestion. Reactive silicon was determined using the method of ascorbic acid reduction to molybdenum blue. Filterable reactive phosphorus (FRP) was analyzed by the molybdenum blue/ascorbic acid reduction procedure as modified by Eisenreich et al. (1975). Total phosphorus (TP) utilized the FRP procedure after acid-persulfate digestion. Nitrate + nitrite was analyzed as nitrite following cadmium reduction, and total ammonia utilized the phenylhypochlorite methodology. Total Kjeldahl nitrogen (TKN) was determined as ammonia following acid-block digestion. We computed total nitrogen (TN) as the sum of TKN and nitrate + nitrite.

For analysis of chlorophyll *a* (chl *a*), we filtered 1-2 L aliquots of each water sample through a GFF filter to which we added 2 ml of MgCO₃ just prior to completion of the filtration process. Individual filters were stored frozen in separate plexiglas slides until analyzed. We extracted algal pigments by grinding the filters with a Teflon pestle in 90% acetone and refrigerating (4°C) the slurry in the dark for 2 hr. Following acetone extraction, the slurry was centrifuged and the supernatant was decanted and brought to volume with 90% acetone. Chl *a* concentration (corrected for inactive phaeophytin) was determined using a calibrated (Sigma Co. chl *a* standards) Turner model 112 fluorometer.

Vertical zooplankton tows were collected using a 0.2-m diameter, conical zooplankton net constructed with a 153-μm mesh. Zooplankton hauls were pulled manually from 50 m to the surface or from the bottom if the depth was less than 50 m at approximately 0.5 m sec⁻¹ and the contents preserved in 10% buffered formalin. Zooplankton were counted, identified, and measured using a binocular dissecting microscope. Body length was measured as described in Koenings et al. (1987). Zooplankton biomass was calculated using species-specific regression equations relating mean length to dry mass as described

in Koenings et al. (1987). We expressed zooplankton density and biomass on a per-unit-lake area basis (Nr. m^{-2} or mg m^{-2}) rather than on a volumetric basis because the latter implies a uniform vertical distribution. Use of areal (per-unit-area) estimates of crustacean abundance and biomass in aquatic studies are commonly reported in the scientific literature.

To assess the magnitude of zooplanktivory or grazing pressure in Becharof and Ugashik lakes, we made the assumption that the number of spawners was proportional to fry recruitment. We then devised a composite index of grazing pressure based on spawner density and macrozooplankton community characteristics. Our index of grazing pressure was simply computed as the escapement per unit of lake area or spawner density (Nr. km^{-2}) divided by the seasonal mean areal zooplankton biomass (kg km^{-2}) estimate. Thus, the grazing pressure index is expressed as the number of spawners per unit standing stock macrozooplankton (Nr. kg^{-1}). We assumed that high values are associated with increased grazing pressure or conversely low values reflect low sockeye planktivory. For comparative purposes, we also computed the grazing pressure index for 10 other Alaskan sockeye nursery lakes. Like the Becharof and Ugashik data sets, the grazing pressure index for these lakes was calculated using only the brood year escapements in which we had corresponding zooplankton data from the subsequent rearing year.

Climatological Data

Time series of terrestrial air temperatures and precipitation for King Salmon, Alaska was obtained from the U.S. National Climate Data Center (Crawford 2000). For each month, we subtracted the year-specific monthly mean temperature from the mean monthly temperature averaged over all available years (1968-1999) to give monthly temperature anomalies. Monthly temperature anomalies were subsequently plotted by individual year. To assess the underlying trends in the time series, the data were fitted using the LOWESS procedure (*see* Statistical Analysis).

Statistical Analysis

To test for spatial differences in water chemistry, nutrient concentrations, and algal pigment levels we used analysis-of-variance (ANOVA) with station and year as categorical variables followed by Tukey's pairwise post hoc comparisons. In the spatial analysis, we considered data derived for the 1-m stratum, which were taken as the year-specific station means. The LOWESS smoothing procedure was used to assess the underlying relationship between two variables and possible trends in time-series data. The LOWESS routine calculates a new smoothed y-value for each x-value without imposing a functional form on the data. We used correlation (Pearson's) analysis to assess whether two variables could be related by a linear function. The correlation coefficient (r) assumes a value between -1 and +1. If one variable tends to increase as the other decreases, the correlation coefficient is negative. Conversely, if the two variables tend to increase together the correlation coefficient is positive. Correlations equal to -1

or 1 indicate one variable can be predicted from another perfectly by a linear function of the other. Least squares regression analysis was used to test the functional relationship between two variables. Other fits such as quadratic or power models were applied when examination of the residuals from a linear regression indicated a linear relationship was not entirely appropriate (Neter et al. 1990). Adult stock-recruitment data were initially fitted to the Ricker (1975) model by transforming the equation $R = aS[\exp]^{-bS}$ into the form $\ln \left(\frac{R}{S} \right) = a - bS$, and treating it as a linear regression, where R is total returns, S is the number of spawners, a is the intercept, and b is the slope (Hilborn and Walters 1992). We also conducted a Ricker analysis using the data for parental escapement and the resultant smolt abundance estimates. All statistical tests were conducted at a significance level of 5% using SYSTAT version 9 (SPSS 1998).

RESULTS

Stock and Recruitment Patterns

A similarity existed between Egegik and Ugashik River sockeye relative to temporal patterns in spawner abundance (Figure 5a), adult recruits (Figure 5b), and recruitment rate, i.e. recruits-per-spawner (R/S) (Figure 5c) as a function of brood year. A LOWESS smoothing procedure revealed distinct brood-year periods of a pre-buildup (1956-1973), increase or build-up (1974-1987), and then a leveling off or decline (1988-1995) common to both lakes. The average number of spawners, total returns, and return-per-spawner for the three periods are shown below:

<u>River System</u>	<u>Period</u>	<u>Number of Spawners</u>	<u>Total Return</u>	<u>Return/Spawner</u>
Egegik River	1956-1973	825,000	2,522,000	3.2
	1974-1987	989,000	8,910,000	9.0
	1986-1995	1,854,000	9,829,000	5.3
Ugashik River	1956-1973	470,000	867,000	2.1
	1974-1987	976,000	4,445,000	8.1
	1988-1995	1,453,000	3,624,000	3.2

The peak R/S (9) for Egegik sockeye occurred during the 1974-1987 period, which corresponded to a mean escapement of 990,000. In comparison, peak R/S for Ugashik sockeye (8) occurred during the same time period with a mean escapement of approximately 980,000.

The regression of $\ln R/S$ on S (i.e., transformation of the classic Ricker model) did not describe the S - R data for either the Egegik ($P = 0.804$) or Ugashik ($P = 0.405$) sockeye data sets (Figure 6a-b). In addition, LOWESS did not reveal any obvious pattern or trend. For the Ugashik data set, eight of the points fell below replacement, i.e. $\ln R/S$

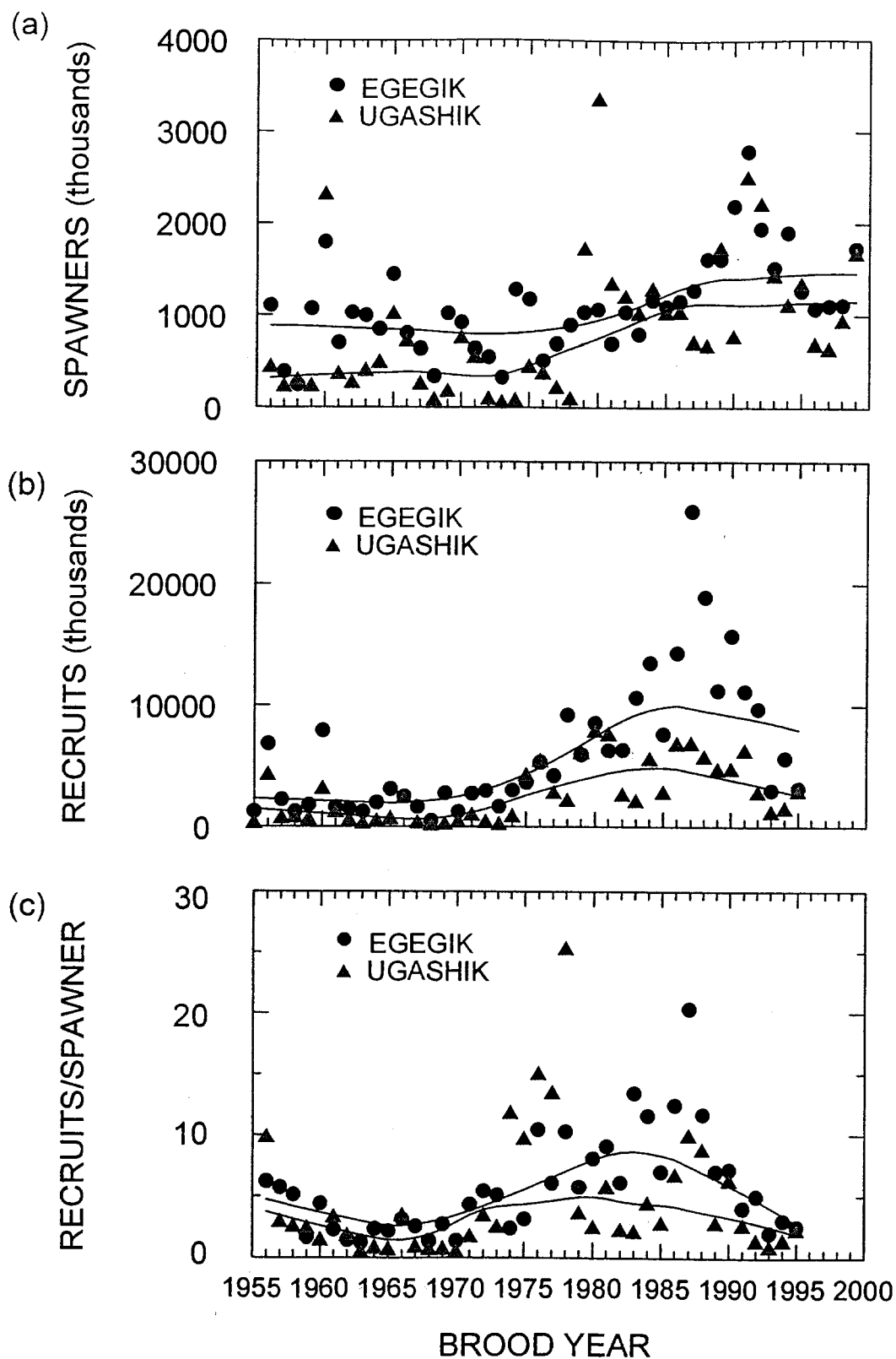


Figure 5. Temporal pattern in (a) size of spawning stock, (b) adult recruits, and (c) recruits-per-spawner for Egegik and Ugashik sockeye, brood years 1956-1995. Solid lines are LOWESS smoothed fits.

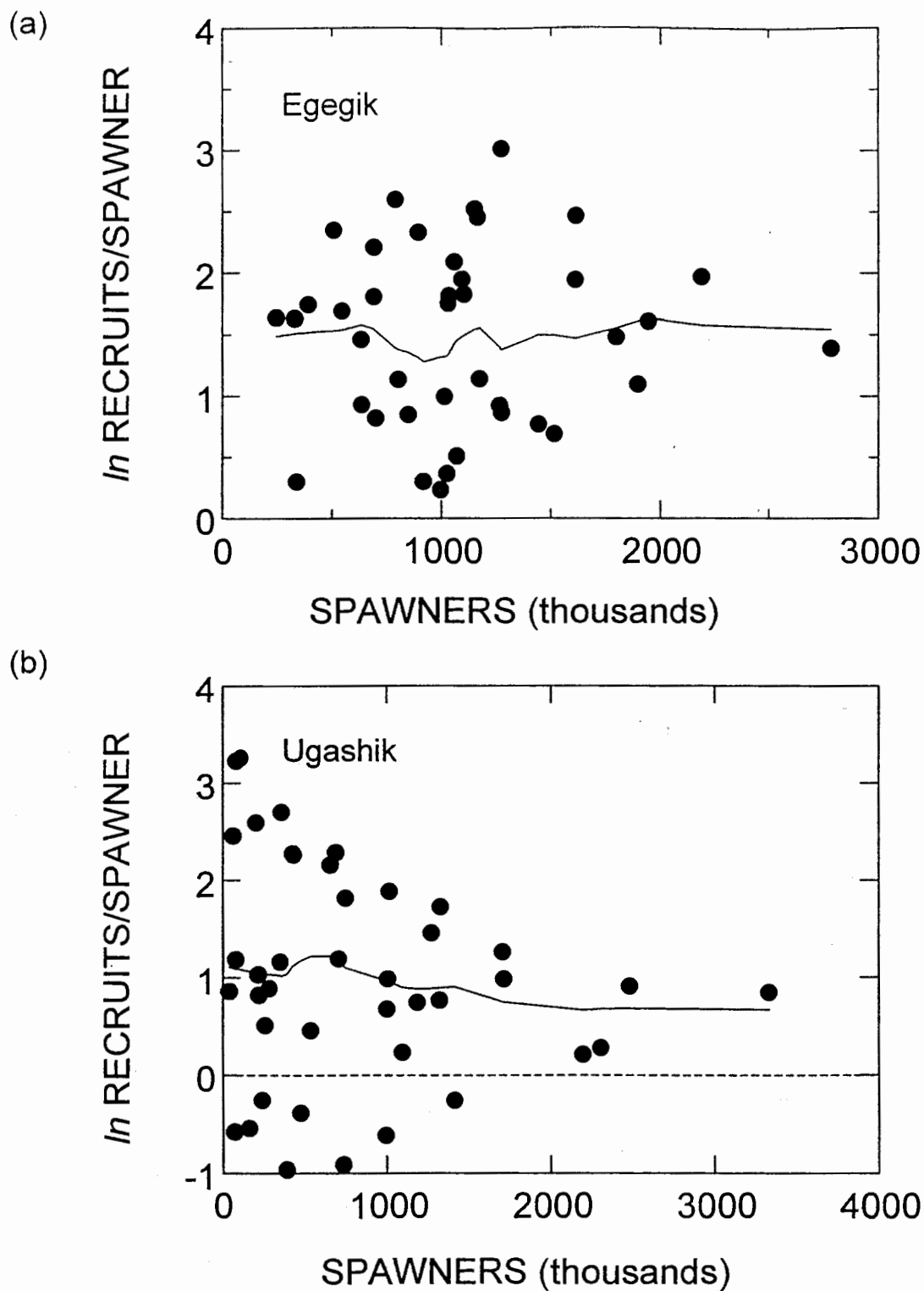


Figure 6. Plot of natural logarithm (\ln) of sockeye adult recruits-per-spawner against spawner abundance for (a) Egegik and (b) Ugashik rivers, brood years 1956-1995. The solid lines show LOWESS smoothed fits and the dashed line indicates replacement (spawners = returns).

values were less than zero. For both stocks recruitment was roughly proportional to spawner abundance, though the variation explained (r^2) was small. That is, the S-R relationships for Egegik (Figure 7a) and Ugashik (Figure 7b) sockeye appeared to resemble density-independent survival. Thus, management parameters such as spawners to maximize yield and spawners to maximize returns could not be estimated in the usual manner.

A summary of the Markov probability matrices indicated that for Egegik sockeye the highest surplus yield (11 million) occurred when the spawner abundance was in the range of 1.5-1.8 million (Table 1); however, high yields (8.3-9.3 million) also resulted from escapements in the range of 1.05-1.5 million, which corresponded with the highest average recruitment rate (8.3). Escapements exceeding 1.8 million resulted in high yields (nearly 11 million) coupled with a halving of the recruitment rate, though there were few observations in this range. For Ugashik sockeye the highest yield (5.2 million) occurred when brood year escapements were in the range of 1.2-1.5 million. For escapements of 900,000 or less, the range in recruitment rate (4.4-5.7) was relatively consistent, whereas escapements above 900,000 resulted in a lower and more variable recruitment rate (2.5-5.0).

A quadratic model best described ($r^2 = 0.82$) the relationship between mean yield and mean spawner abundance for the Egegik data (Figure 8a). The curve peaked at a yield of approximately 11.0 million, equivalent to a mean escapement of 2.6 million. However, these data represented the upper end of the range in our spawner abundance data. The left half of the data was nearly linear up to a yield of about 4.5 million, corresponding to an average escapement of about 1.0 million. For the Ugashik sockeye data set a quadratic function was also the best fit ($r^2 = 0.60$) (Figure 8b). Mean yield peaked at about 3.8 million, corresponding to an escapement of 1.7 million. However, the curve began to decelerate at an average escapement of approximately 650,000, matching a mean yield of approximately 2.4 million sockeye.

Smolt Abundance and Age Composition

For Egegik sockeye, the 1999 smolt population estimate was the lowest observed since sonar enumeration began, totaling 8.6 million smolts (Figure 9a). However, in 1999 ice break-up of Becharof Lake was later than usual, hence the smolt abundance estimate was probably conservative. In comparison, the 1989 outmigration was an estimated 100 million smolts. Over the available time series, the annual average proportion of age 1 smolts varied from less than 10% to more than 80% (Figure 9b). In the three years (1983, 1992, and 1999) of lowest production (<30 million), age 2 smolts were the dominant (80-90%) age class. However, when total smolt abundance exceeded 60 million, age 2 smolts accounted from 70 to 97% of the population. For Ugashik sockeye, smolt production declined from approximately 215 million in 1988 to an annual production of approximately 10 million during 1997-1999, (Figure 10a). Since 1982, the proportion of age 1 smolts ranged from 20% to 97%; however, in the last three years of

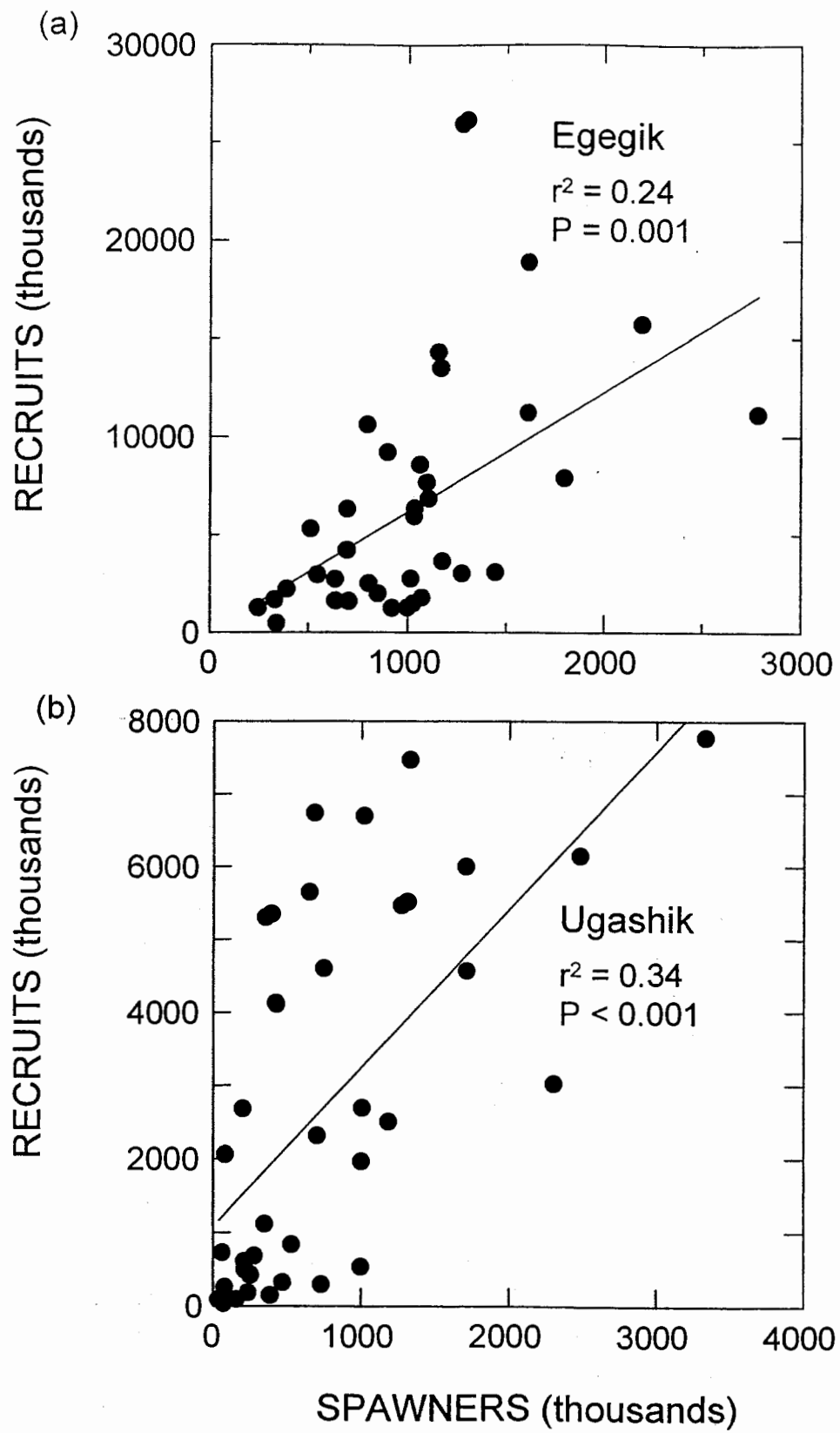


Figure 7. Adult recruits as a function of spawners for (a) Egegik and (b) Ugashik sockeye salmon. Solid lines are linear fits to the data.

Table 1. Summary of results from two Markov transition probability tables of Egegik and Ugashik River sockeye salmon spawner-recruit data, 1956-1995. Each table was based on a spawner abundance interval of 300,000 fish and the tables were offset by 150,000 fish. Spawner intervals and means are given in thousands of fish.

System	Spawner interval	<i>N</i>	Mean spawners	Mean recruits	Recruits/spawner	Mean yield
Egegik	0-300	1	246	1,263	5.1	1,017
	150-450	4	327	1,409	4.3	1,083
	300-600	5	423	2,530	5.6	2,107
	450-750	7	631	3,535	5.7	2,904
	600-900	9	745	4,535	5.9	3,791
	750-1,050	10	937	4,336	4.8	3,399
	900-1,200	13	1,065	5,801	5.3	4,736
	1,050-1,350	9	1,153	9,486	8.1	8,334
	1,200-1,500	3	1,332	10,693	8.3	9,362
	1,350-1,650	3	1,557	11,083	6.9	9,526
	1,500-1,800	3	1,675	12,686	7.7	11,011
	1,650-1,950	2	1,873	8,805	4.7	6,933
	>1,800	3	2,308	12,000	5.3	9,892
Ugashik	0-300	12	159	696	5.6	537
	150-450	12	294	1,666	5.1	1,372
	300-600	7	421	2,282	5.7	1,861
	450-750	7	647	2,968	4.4	2,320
	600-900	5	706	3,923	5.7	3,217
	750-1,050	4	1,005	2,974	2.9	1,969
	900-1,200	5	1,041	2,881	2.8	1,840
	1,050-1,350	3	1,261	5,147	4.0	3,885
	1,200-1,500	2	1,299	6,466	5.0	5,167
	1,350-1,650	0	--	--	--	--
	>1,500	5	2,308	5,508	2.5	3,200

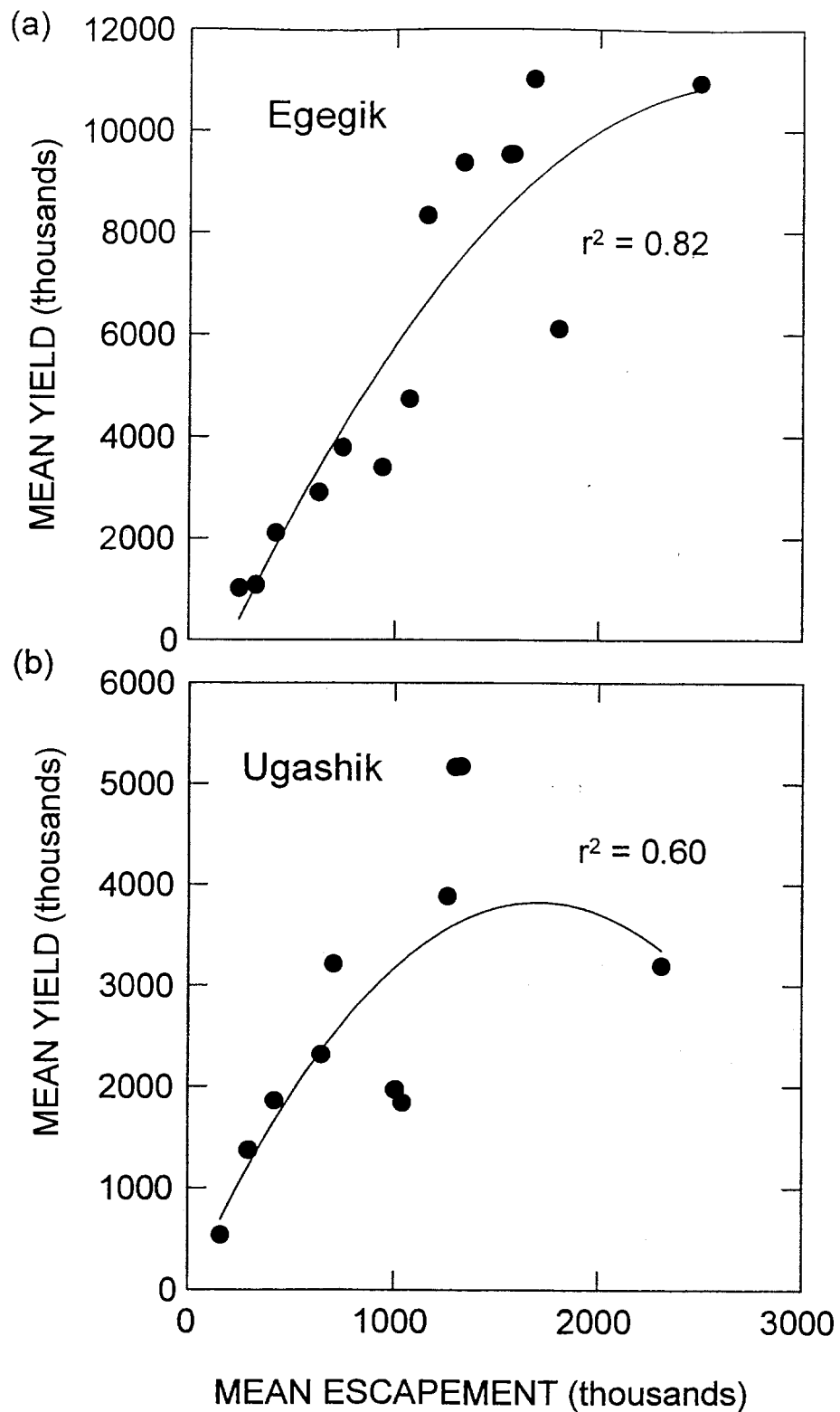


Figure 8. Plot of results of the tabular analysis of spawner-recruitment data showing a curvilinear relationship between mean yield and escapement for (a) Egegik and (b) Ugashik sockeye salmon. A quadratic curve was fitted to both data sets.

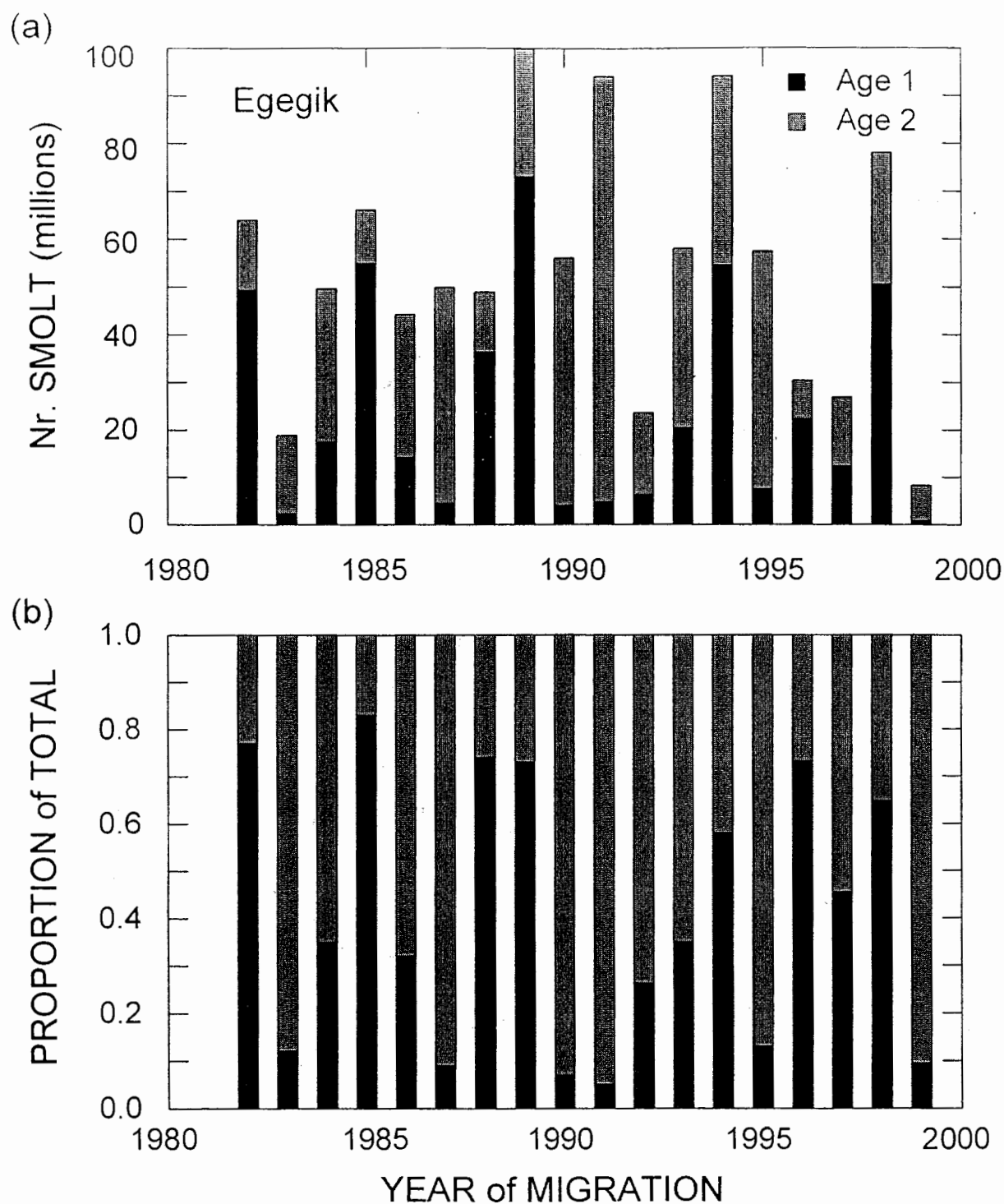


Figure 9. Estimates of (a) smolt abundance and (b) age composition by year of migration for Egegik sockeye salmon, 1982-1999.

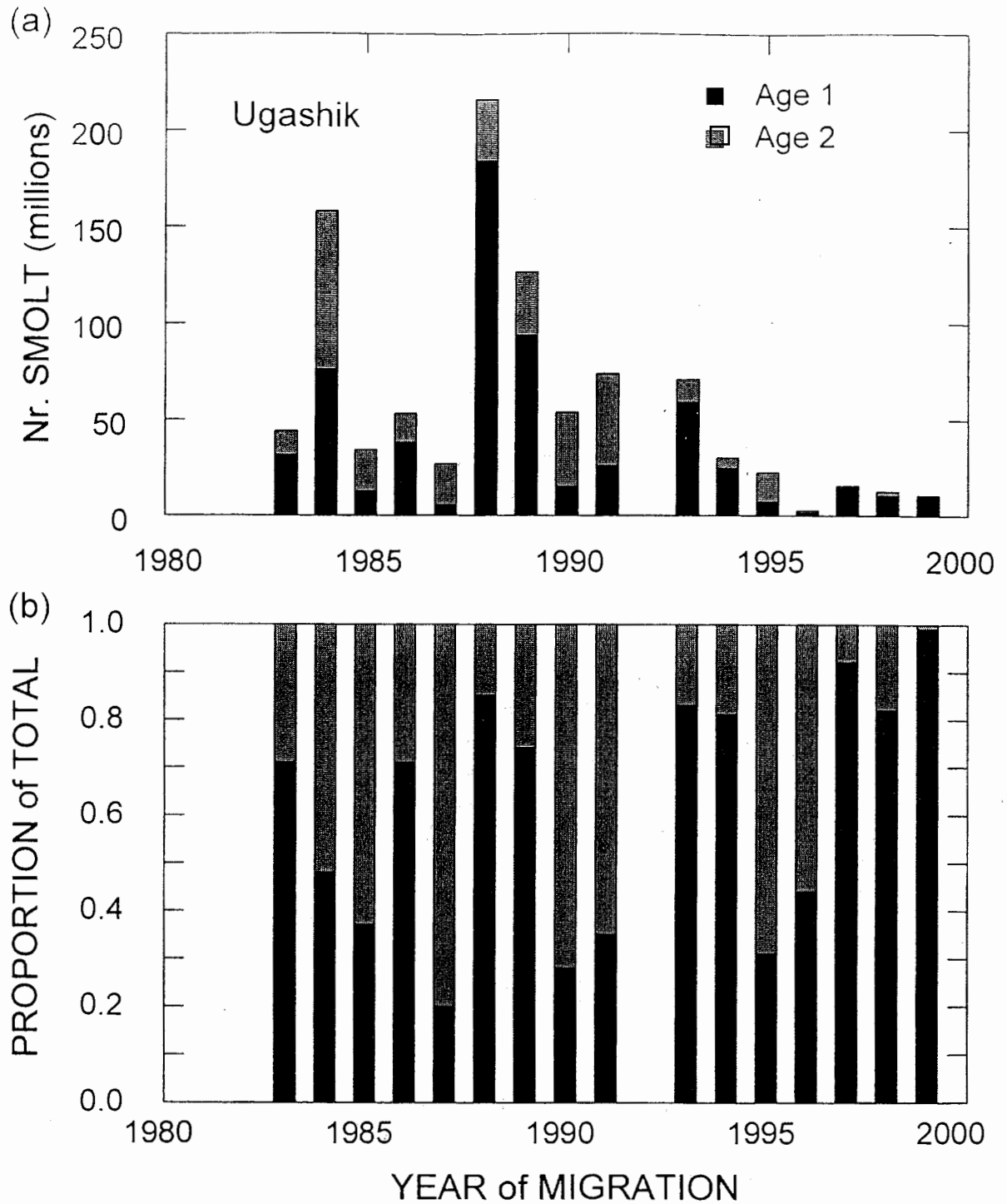


Figure 10. Estimates of (a) smolt abundance and (b) age composition by year of migration for Ugashik sockeye salmon, 1983-1999. The smolt enumeration project was not conducted in 1992.

low abundance, age 1 smolts composed more than 80% of the population (Figure 10b). Both systems produce few age 3 smolt, but their contribution was usually less than 1%. The temporal changes in smolt production in the Egegik River by brood year revealed a rough 4-5 year cycle (Figure 11a), which was also seen in terms of the recruitment rate (Figure 11b). In addition to the quasi-cyclic pattern, the underlying trend appeared to be a decline beginning with brood year 1983. There was no apparent relationship between the size of parental stock and the resultant number of smolts produced (Figure 11c). The regression of \ln smolts-per-spawner against spawners (Figure 11d) was not significant at our prescribed significance level ($\alpha=0.05$). However, the slope was significant at the 10% significance level ($r^2=0.19$; $F=3.2$; $P=0.096$). Although cycling associated with smolt production by brood year was not evident in the Ugashik data set (Figure 12a), recruitment showed a steep decline beginning with brood year 1986 (Figure 12b), though data for brood years 1989 and 1990 were not available. In addition, total smolt abundance was unrelated to the size of the parental stock (Figure 12c). The Ricker curve relating \ln smolts-per-spawner and spawner abundance was not significant ($r^2=0.12$; $F=1.5$; $P=0.25$), even though the trend appeared negative (Figure 12d). Thus, for both Egegik and Ugashik sockeye, smolt abundance and recruitment from spawners to smolt appeared largely independent of the number of spawners.

For the Egegik sockeye, we re-examined the model developed by Martin and Lloyd (1996). First, there was no apparent relationship between the proportions of age 2 holdovers with increasing escapement as evidenced by the LOWESS fit (Figure 13a). Second, we re-plotted the total number of smolts produced in a given brood year (BY) versus the proportion of age 2 smolts produced in the next brood year (BY+1) using five additional data points (brood years 1992-1996). Unlike the original model, which used raw percentage values, we transformed (arcsine square root) the dependent variable (percentage of age 2 smolts) as required in regression analysis involving data expressed as proportions. We found a significant ($P=0.045$), albeit weak ($r^2=0.26$; $F=4.8$), positive relationship between total smolt (BY) and the percentage of age 2 smolts (BY+1) (Figure 13b). However, our regression model explained 3% less variation in the proportion of holdovers than that of the original model. For the Ugashik sockeye data, total smolt produced by one brood year was unrelated ($P=0.49$) to the proportion of holdovers produced by the subsequent brood year.

There was a significant linear relationship ($r^2=0.44$; $P=0.014$) between the total number of smolt and subsequent adult recruits for the Egegik system (Figure 14a). The scatter plot indicated that beyond a total output of 75 million smolts the variability in adult recruitment increased. Data fitted to a power model ($r^2=0.63$; $P=0.014$) showed that adult recruits-per-smolt decreased continuously up to a smolt output of approximately 50 million, beyond which the curve began to flatten out (Figure 14b). For the Ugashik sockeye data set the relationship between adult recruits and total smolts (Figure 14c) was nearly as strong ($r^2=0.42$; $P=0.085$) as that for the Egegik relationship; however, the slope (0.02) was only about one fifth of the magnitude compared to the Egegik relationship (0.11). Adult recruits-per-smolt was inversely related to the number of smolts produced, though the P -value of the regression ($P=0.066$) slightly exceeded our prescribed significance level ($\alpha=0.05$) (Figure 14d). Thus, there appeared to be some

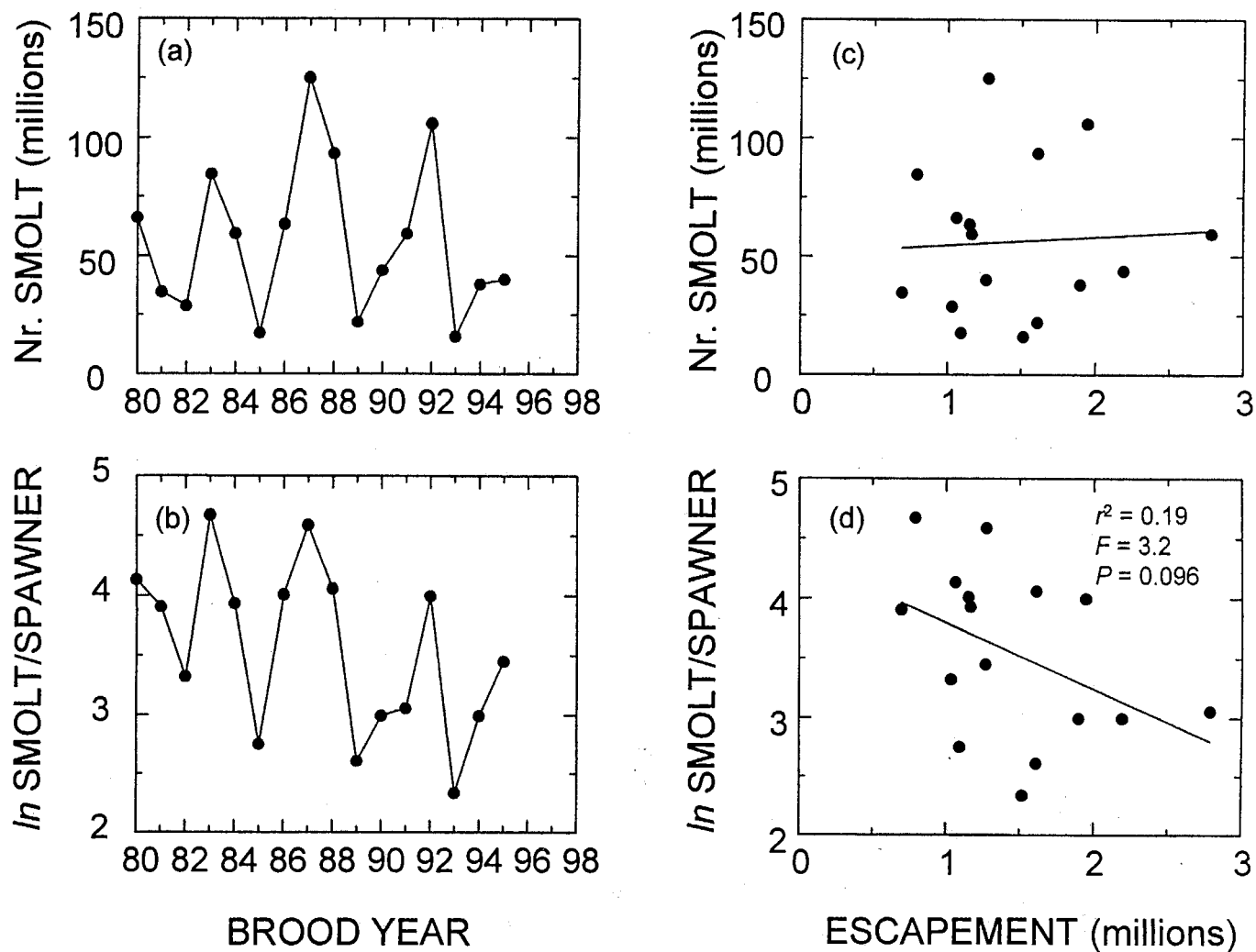


Figure 11. Egegik River sockeye salmon escapement and smolt production plots, brood years 1980-1995; (a) number of smolts produced by brood year, (b) natural logarithm smolts-per-spawner plotted by brood year, (c) number of smolts produced plotted against escapement with corresponding regression line, (d) natural logarithm smolts-per-spawner plotted against escapement with corresponding regression line.

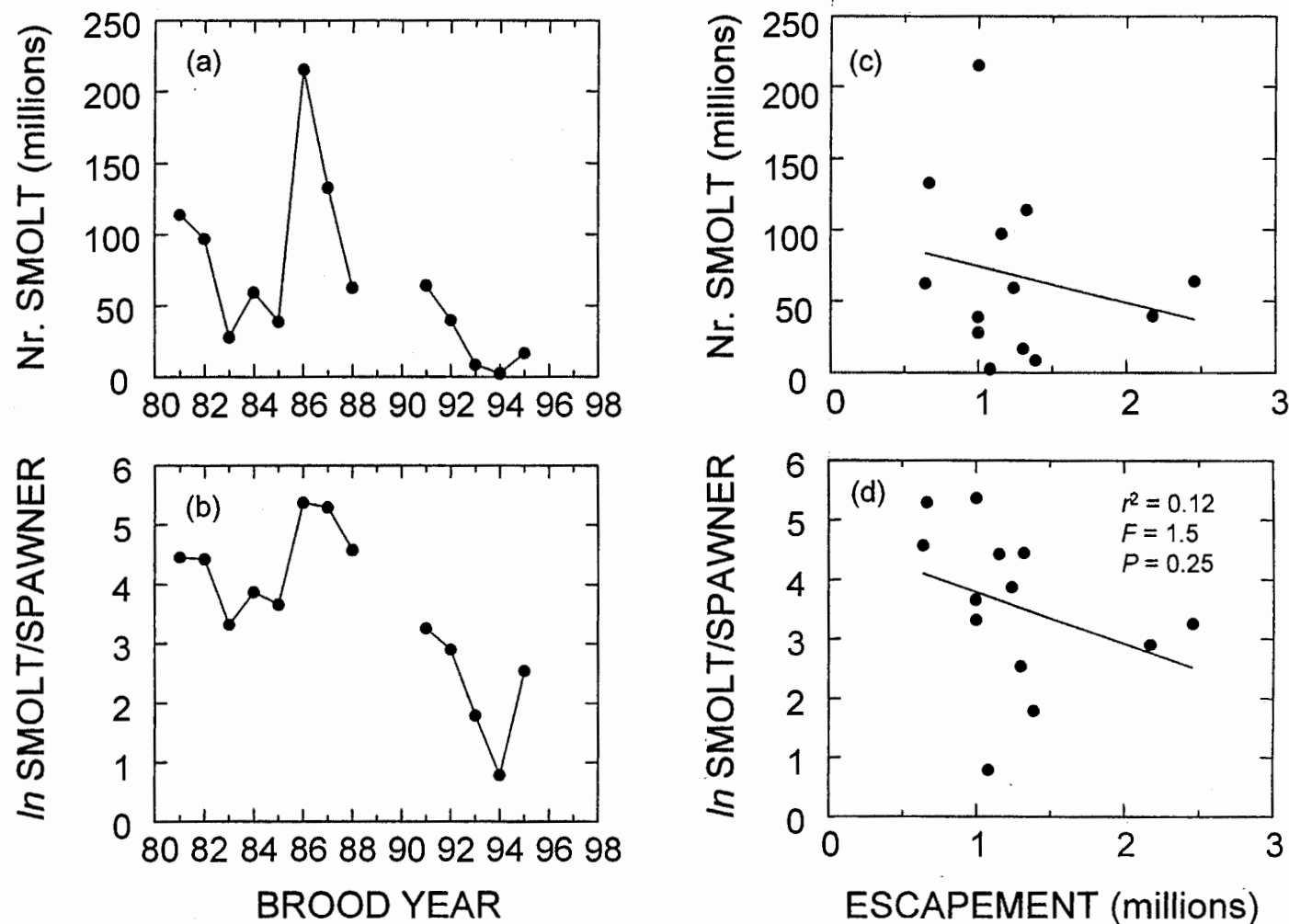


Figure 12. Ugashik River sockeye salmon escapement and smolt production plots, brood years 1981-1995; (a) number of smolts produced by brood year, (b) natural logarithm smolts-per-spawner plotted by brood year, (c) number of smolts produced plotted against escapement with corresponding regression line, and (d) natural logarithm smolts-per-spawner plotted against escapement with corresponding regression line.

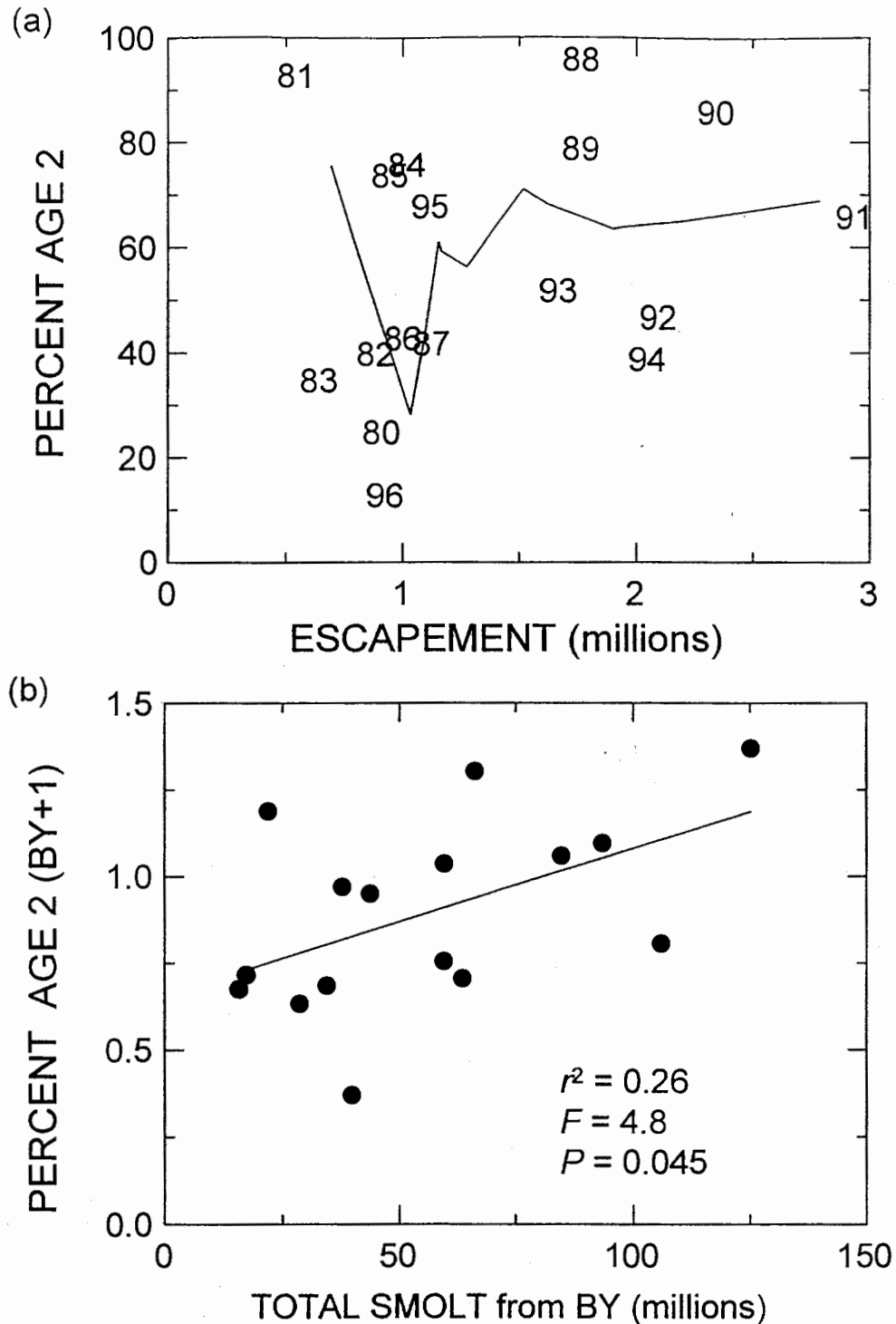


Figure 13. Percent of age 2 sockeye smolts from the Egegik River plotted against brood year escapement (a), the solid line showing a LOWESS-smoothed fit; and (b) relationship between the total number of smolts produced in one brood year (BY) versus the percent of age 2 smolts in the subsequent brood year (BY+1), the solid line showing a linear fit following arcsine transformation of the dependent variable.

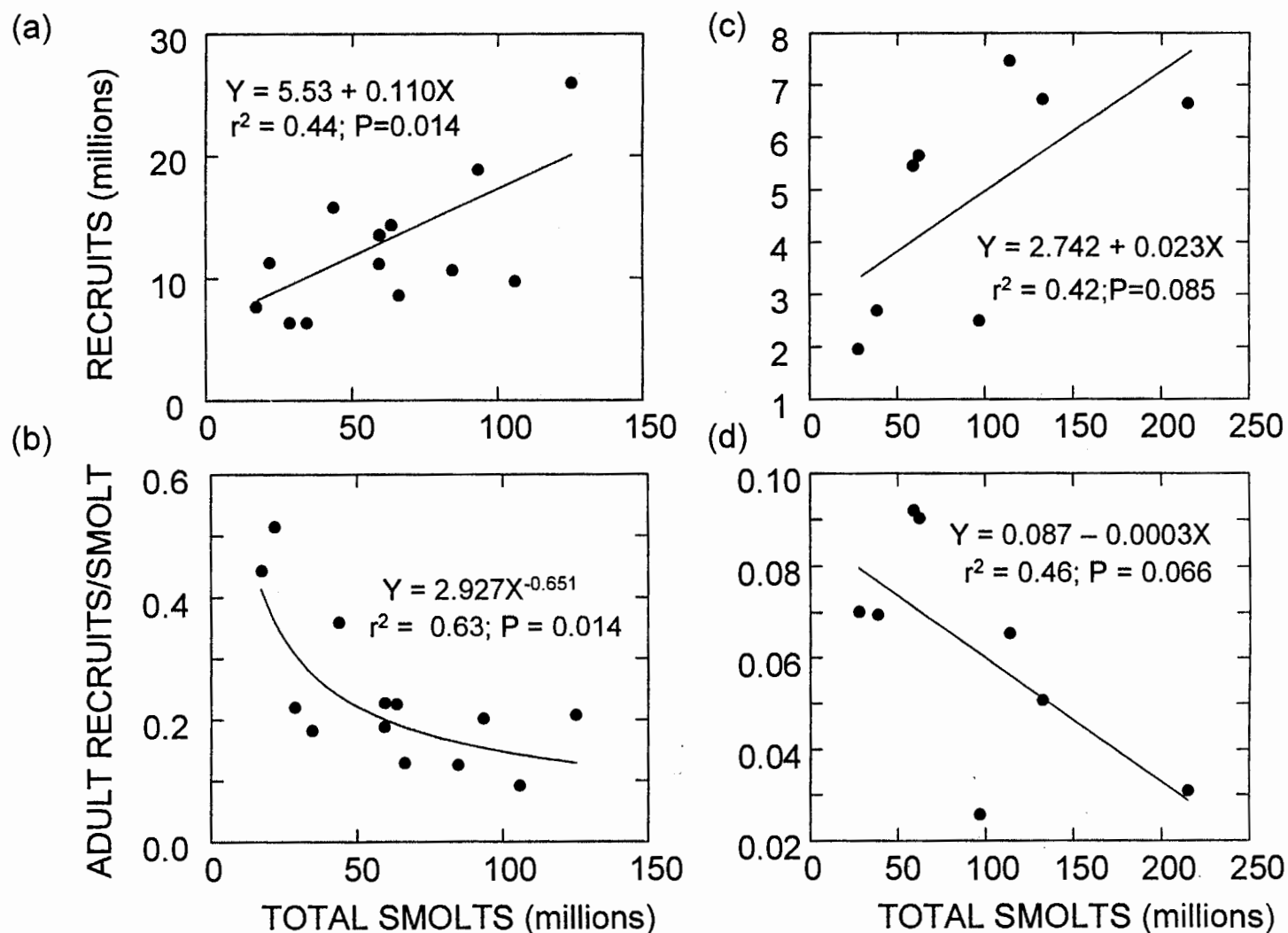


Figure 14. The relationship between (a) the total number of smolts and subsequent adult recruits for Egegik sockeye, (b) the total number of smolts and adult recruits-per-smolt for Egegik sockeye, (c) as in "a", except for Ugashik sockeye, and (d) as in "b", except for Ugashik sockeye.

evidence of a density dependent mechanism(s) affecting smolt-to-adult-survival in both Egegik and Ugashik sockeye stocks.

Smolt Size

For Egegik sockeye, the mean population length of age 1 smolts varied from 87 to 107 mm (Figure 15a), while the mean weight ranged from 6.1 to 11.6 g (Figure 15b). In comparison, age 2 smolt lengths ranged from 105 to 130 mm, and the mean weight varied from 10.5 to 17.1 g. Although mean sizes were fairly consistent, the 1990 data point appeared as an obvious outlier in the time series. The Ugashik system typically produced smaller size sockeye smolts than the Egegik system. The mean length of age 1 smolts ranged from 87 to 101 mm (Figure 16a), while the mean weight ranged from 5.7 to 9.9 g (Figure 16b). The average length of age 2 smolts ranged from 102 to 125 mm and mean weight varied from 10.3 to 17.5 g. For the Egegik data, there was a significant negative correlation between age 1 length ($r = -0.69$; $P=0.36$) and weight ($r = -0.61$; $P = 0.13$) and the total number of smolts (Figure 17). Linear regression produced the following significant inverse relationships: $Age\ 1\ Length = 107.9 - 0.872 \times Total\ Smolt$ ($r^2 = 0.47$; $P=0.004$) and $Age\ 1\ Weight = 10.87 - 0.22 \times Total\ Smolt$ ($r^2 = 0.37$; $P=0.013$). However, most of the variation in the two models was unexplained and the slopes were highly influenced by the single point corresponding to the 1990 outmigration. Correlations between age 2 smolt length ($P = 0.912$) and weight ($P=1.0$) and smolt abundance were also negative, but not significant. For the Ugashik data set, correlations between smolt size and abundance were not significant ($P>0.05$) for either age class of smolts (Figure 17). Thus, there was little if any indication that smolts of larger populations neither grew slower nor were they of smaller size than smolts of smaller populations, at least within the range of these data.

Macrozooplankton and Grazing Pressure

The macrozooplankton community of Becharof Lake was similar taxonomically to that of other clear water lakes that support populations of rearing sockeye juveniles. The macrozooplankton of Becharof Lake were divided into three main groups: (1) cyclopoid copepods, (2) calanoid copepods, and (3) cladocerans. Crustacean zooplankton of Ugashik Lake were unlike all other clear water lakes we have examined, composing only cyclopoids and calanoids; i.e., no cladocerans (water fleas) were found in any of the samples. Table 2 presents a list of genus or species present (1997-1999) in Becharof and Ugashik lakes as grouped above. Among the copepods, *Eurytemora* sp. was the largest species in terms of mean body length followed by *Diaptomus pribilofensis* and *Cyclops columbianus*. In Becharof Lake, *Daphnia longerimus* was the largest sized species of the cladoceran group, followed by *Holopedium gibberum*, *Bosmina longirostris*, and *Chydoridae* sp. For a specific taxon, there was little difference in mean zooplankton body size across the three-year study period.

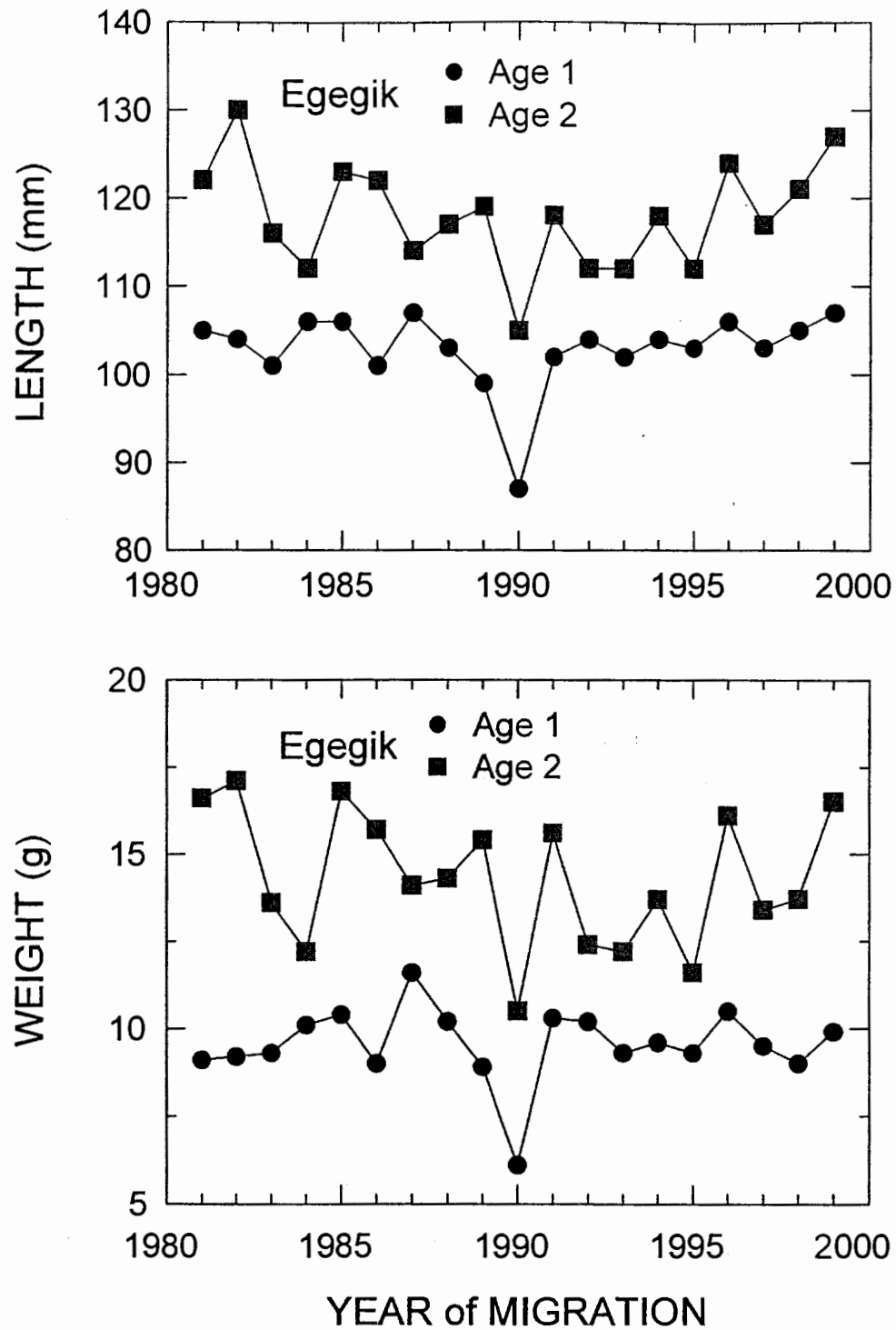


Figure 15. Mean population length and weight of Egegik River sockeye smolt by age class, 1981-1999.

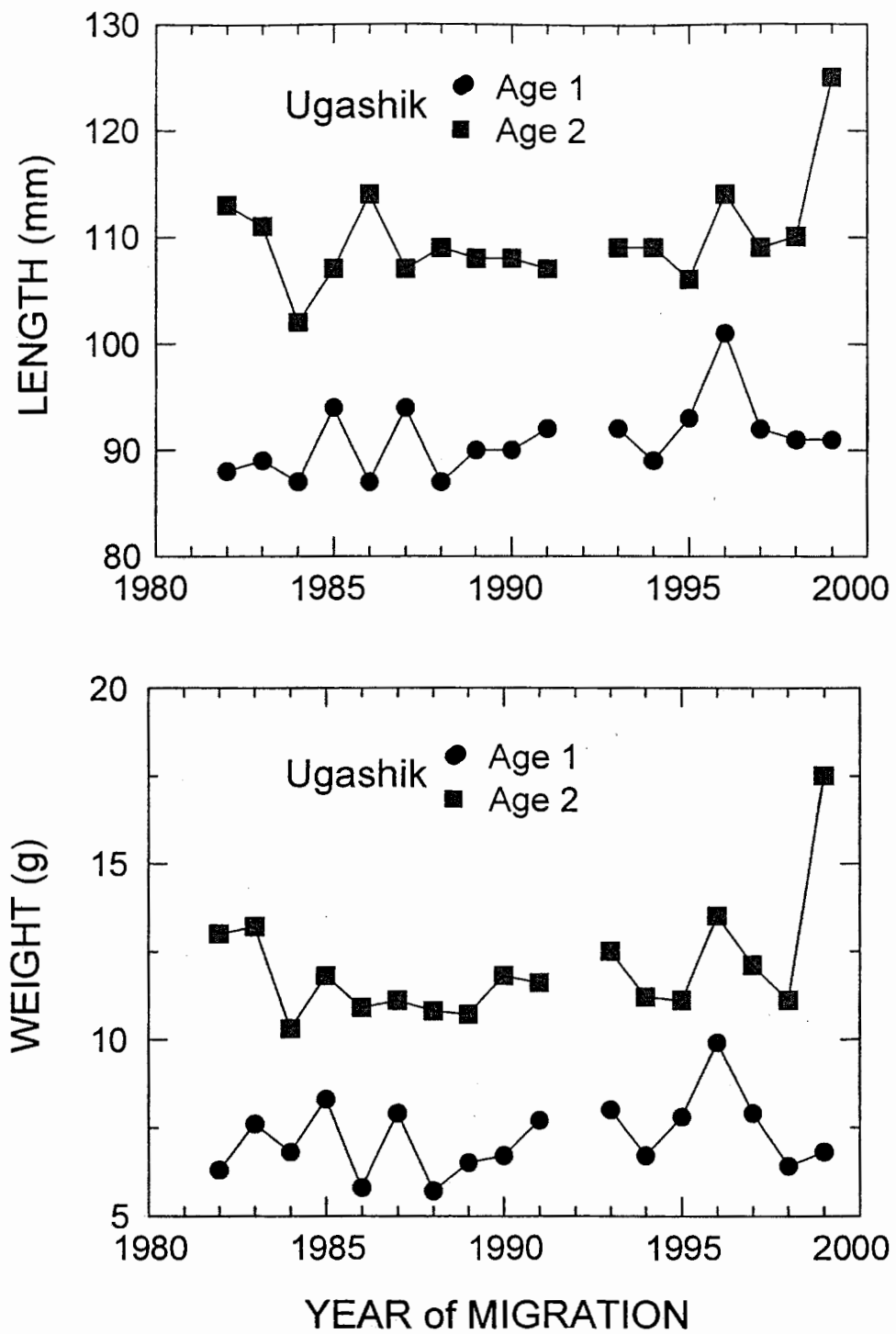


Figure 16. Mean population length and weight of Ugashik River sockeye smolt by age class, 1982-1999. Note that the smolt program was not conducted in 1992.

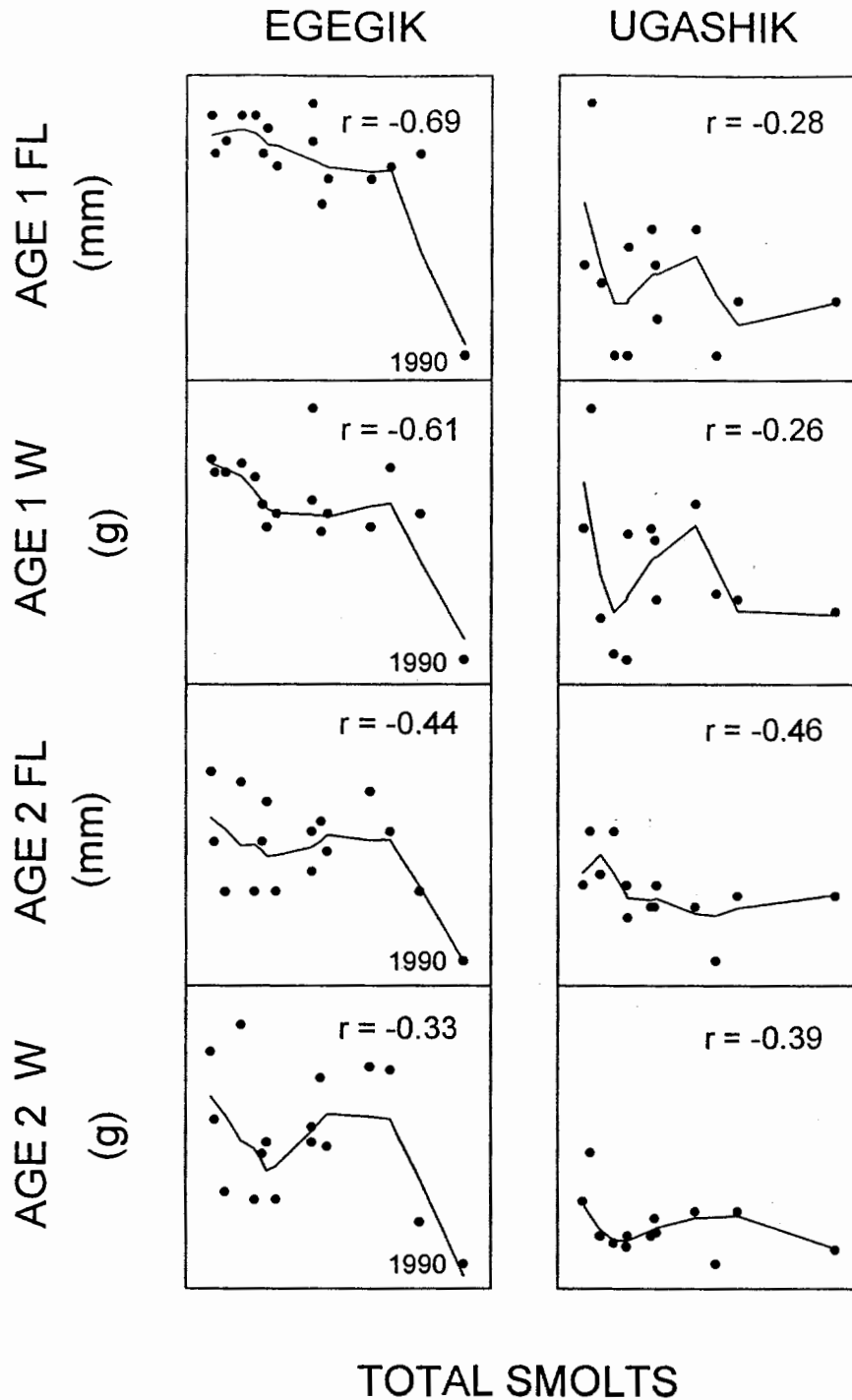


Figure 17. Scatterplot matrix showing the relationship between total sockeye smolt abundance and mean population length (FL) and weight (W) by age class for the Egegik and Ugashik systems. The solid lines are LOWESS fits to the data and the r statistics are Pearson's correlation coefficients. Note the 1990 data for Egegik sockeye smolt are outliers.

Table 2. Mean length (millimeters) of macrozooplankton in Becharof and Ugashik lakes, 1997-1999.

Lake	Group	Taxon	1997	1998	1999
Becharof	Cyclopoid	<i>Cyclops columbianus</i> , non-ovigerous	0.71	0.85	0.72
		<i>Cyclops columbianus</i> , ovigerous	1.22	1.29	1.16
	Calanoid	<i>Diaptomus pribilofensis</i> , non-ovigerous	0.96	0.96	1.02
		<i>Diaptomus pribilofensis</i> , ovigerous	1.24	1.26	1.26
	Calanoid	<i>Eurytemora</i> sp., non-ovigerous	1.08	1.06	1.06
		<i>Eurytemora</i> sp., ovigerous	1.26	1.47	1.26
	Cladoceran	<i>Bosmina longirostris</i> , non-ovigerous	0.37	0.41	0.37
		<i>Bosmina longirostris</i> , ovigerous	0.42	0.47	0.46
	Cladoceran	<i>Daphnia longiremus</i> , non-ovigerous	0.71	0.78	0.70
		<i>Daphnia longiremus</i> , ovigerous	0.94	1.17	0.96
	Cladoceran	<i>Holopedium gibberum</i> , non-ovigerous	0.42	0.45	0.49
		<i>Holopedium gibberum</i> , ovigerous	0.75	0.60	0.60
	Cladoceran	<i>Chydoridae</i> sp., non-ovigerous	0.21	0.28	0.27
		<i>Chydoridae</i> sp., ovigerous	np ^a	0.31	np
Ugashik	Cyclopoid	<i>Cyclops columbianus</i> , non-ovigerous	0.65	0.70	0.69
		<i>Cyclops columbianus</i> , ovigerous	1.12	1.12	1.12
	Calanoid	<i>Diaptomus pribilofensis</i> , non-ovigerous	0.87	0.86	0.93
		<i>Diaptomus pribilofensis</i> , ovigerous	1.05	1.19	1.28
	Calanoid	<i>Eurytemora</i> sp., non-ovigerous	1.03	np	1.36
		<i>Eurytemora</i> sp., ovigerous	1.45	np	np

a/ species not present; no measurement.

During 1997-1999, seasonal mean macrozooplankton densities (Nr. m⁻²) ranged from approximately 207,000 to 362,000 in Becharof Lake (Figure 18a) and from 380,000 to 622,000 in Ugashik Lake (Figure 18b). In Becharof Lake, *Cyclops* made up the largest percentage (42-48%) of the seasonal mean total density (Figure 18c). Calanoids and cladocerans attained lesser densities, composing from 22 to 27% and from 21 to 33% of the seasonal average density, respectively. In Ugashik Lake, 60-74% of the seasonal average density was composed of *Cyclops*; the rest (26-40%) of the density was made up of calanoids (*Diaptomus* and *Eurytemora*) (Figure 18d). The seasonal mean macrozooplankton biomass (mg m⁻²) ranged from 626 to 892 in Becharof Lake (Figure 19a), while higher biomass levels were found in Ugashik Lake, ranging from 872 to 1,364 (Figure 19b). In terms of biomass, however, calanoids clearly dominated the macrozooplankton community in both lakes. Calanoids made up from 44 to 55% of the total biomass in Becharof Lake, whereas cyclopoid and cladoceran assemblages made up smaller proportions, ranging from 30 to 42% and from 13 to 25%, respectively (Figure 19c). In Ugashik Lake, calanoids represented from 40 to 59% of the total biomass, however, in 1998 mean biomass of cyclopoids (526 mg m⁻²; 60%) was greater than calanoids (346 mg m⁻²; 40%) (Figure 19d).

Seasonal changes in density, biomass, and mean body length by sample station for each major taxonomic group are presented for Becharof and Ugashik lakes, respectively in Appendices A and B. For Becharof Lake, cyclopoid and calanoid density and biomass at stations 2 (Island Arm) and 3 (Ruth Arm) were considerably lower throughout the season compared to the other stations. In contrast, cladoceran density and biomass were higher at stations 2 and 3 compared to the other sampling sites. There was no apparent difference with respect to mean body size for a given zooplankton group among stations. We found little or no difference in mean length, density or biomass for any of the major zooplankton groups across stations in Ugashik Lake.

During our three-year study, escapements averaged 961 spawners per square kilometer (Nr. km⁻²) for Becharof Lake and 1,931 for Ugashik Lake. In comparison, the spawner density for 10 other selected Alaskan lakes averaged 7,800 (Table 3). Among these systems, Karluk Lake (Kodiak Island) had the highest mean spawner density (16,000), whereas Tustumena Lake (Kenai Peninsula) had the lowest (734). For 10 other lakes, the average grazing pressure index varied from 7 to more than 800. The 12 lake systems fell into three levels of grazing pressure: 1) average index less than 5 (low), 2) mean index between 5 and 20 (moderate), and 3) mean index greater than 20 (high). The average grazing pressure index for both Becharof and Ugashik lakes was less than 2.

Water Chemistry, Nutrients, and Chlorophyll a

A summary of water chemistry, nutrient concentrations, and chlorophyll levels for both study lakes are presented in Table 4. The pH of both the lakes hovered around neutrality and the alkalinity (inorganic carbon) was very low. In addition, average calcium and magnesium concentrations were nearly twice as much in Becharof Lake compared to Ugashik Lake. In both lakes, color never exceeded 15 Pt units, while the maximum

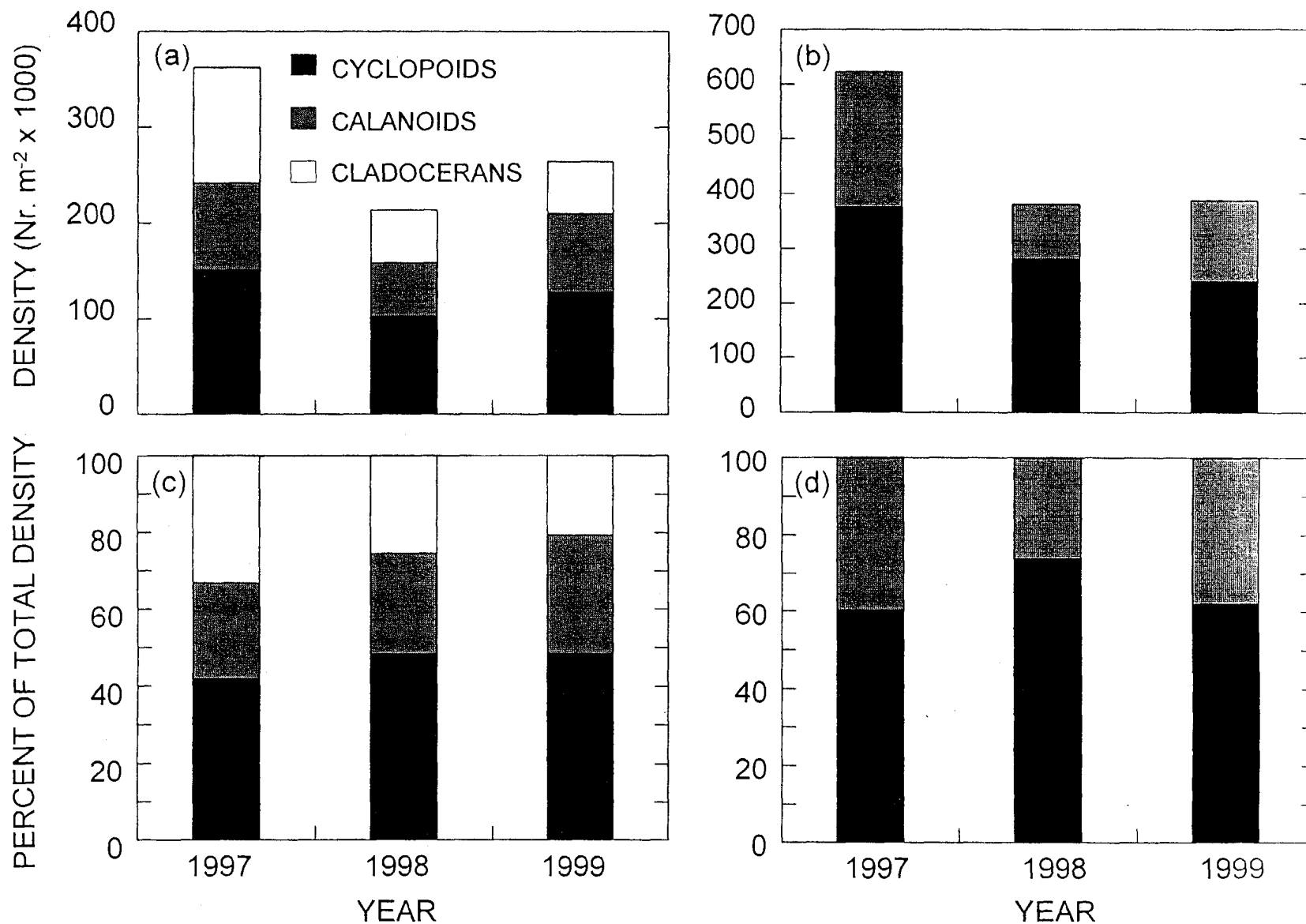


Figure 18. Average macrozooplankton abundance by major taxonomic group for (a) Becharof Lake and (b) the Ugashik lakes, 1997-1999; and the relative abundance for (c) Becharof Lake and (d) the Ugashik lakes.

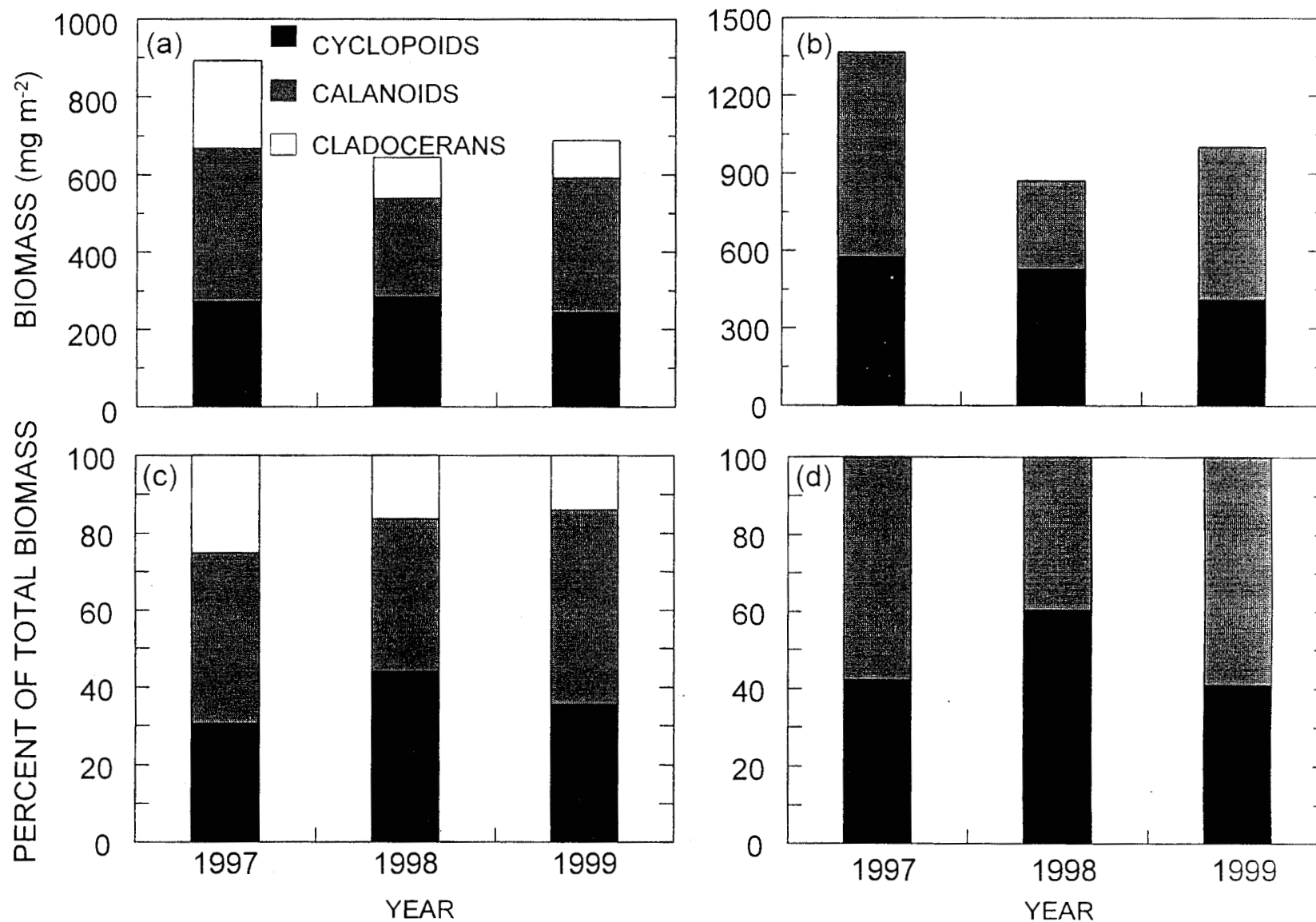


Figure 19. Average macrozooplankton biomass by major taxonomic group for (a) Becharof Lake and (b) the Ugashik lakes, 1997-1999; and the relative biomass for (c) Becharof Lake and (d) the Ugashik lakes.

Table 3. Comparison of mean spawner abundance, spawner density, zooplankton biomass, and grazing pressure index for 12 sockeye nursery lakes.

Lake	Typology	Area (A) (km ²)	Brood years	Mean spawner abundance (P) (Nr.)	Mean spawner density (P/A) (Nr. km ⁻²)	Zooplankton biomass (ZB) (kg km ⁻²)	Grazing pressure index (P/A)/(ZB) (Nr. kg ⁻¹)
Desire	Clear	1.8	1981, 1986	13,200	7,333	17	822.8
Frazer	Clear	16.6	1984-1986	221,963	13,371	149	104.0
Coghill	Glacial	12.7	1987-1997	52,199	4,119	91	89.6
Crescent	Glacial	16.5	1995-1998	69,350	3,212	46	78.9
Karluk	Clear	39.4	1980-1993	601,997	16,370	1,125	17.3
Delight	Clear	2.8	1981, 1986	8,850	3,161	102	37.2
Big	Clear	12.1	1984	75,071	15,785	1,021	15.5
Skilak	Glacial	99.0	1985-1998	422,571 ^a	4,268	485	9.5
Eshamy	Clear	3.6	1980, 1984 1988-1994	29,599	9,503	1,701	7.0
Tustumena	Glacial	294.5	1980-1998	217,048 ^b	734	119	6.8
Ugashik	Clear	381.7	1996-1998	854,954	1,931	1,048	1.9
Becharof	Clear	1142.0	1996-1998	1,103,614	961	767	1.3

a/ The abundance was adjusted to reflect the proportion of spawners to Skilak Lake to the total number of Kenai River mainstem spawners based on fall fry abundance (hydroacoustic) estimates.

b/ A portion of the spawner abundance was back calculated from the number of stocked (spring) fry using standard freshwater survival estimates.

Table 4. Summary of water chemistry, nutrients, and chlorophyll *a* for Becharof and Ugashik lakes, 1997-1999. Data are derived from the 1-m stratum for all stations combined.

Parameter	Units	Becharof Lake			Ugashik Lake		
		Min	Max	Mean	Min	Max	Mean
Conductivity	$\mu\text{mhos cm}^{-1}$	38	95	79	53	68	59
pH	units	6.2	7.3	7.0	6.6	7.6	7.1
Alkalinity	mg L^{-1}	7	21	16	13	20	16
Color	Pt units	2	15	4	3	8	4
Turbidity	NTU	0.2	5.3	1.0	0.3	1.5	0.7
Calcium	mg L^{-1}	3.2	7.6	6.1	3.1	4.7	3.7
Magnesium	mg L^{-1}	0.2	2.4	1.6	0.6	1.6	1.2
Iron	$\mu\text{g L}^{-1}$	10	151	27	6	59	22
Total phosphorus	$\mu\text{g L}^{-1}$	1.6	13.4	5.1	2.3	4.1	4.3
Total filterable phosphorus	$\mu\text{g L}^{-1}$	0.6	6.9	2.6	0.8	7.0	2.1
Filterable reactive phosphorus	$\mu\text{g L}^{-1}$	0.1	5.2	1.3	0.2	3.7	1.6
Total nitrogen	$\mu\text{g L}^{-1}$	49	195	97	78	184	104
Kjeldahl nitrogen	$\mu\text{g L}^{-1}$	45	147.2	82	55	151	88
Ammonia	$\mu\text{g L}^{-1}$	1.7	27.3	10.0	1.6	23.2	7.1
Nitrate+nitrite	$\mu\text{g L}^{-1}$	4	79	15	4	49	16
Reactive silicon	$\mu\text{g L}^{-1}$	197	1,895	605	1,596	3,164	2,379
Chlorophyll <i>a</i>	$\mu\text{g L}^{-1}$	0.09	4.22	0.85	0.14	0.81	0.44

turbidity was about 5 NTU. For the most part, color and turbidity fell below 5 Pt units and 1 NTU, respectively. Both lakes were highly oligotrophic, having low conductivity, total phosphorus (TP) concentrations $<14 \mu\text{g L}^{-1}$, and total nitrogen (TN) $<200 \mu\text{g L}^{-1}$. The average nitrate + nitrite concentrations were 15 and $16 \mu\text{g L}^{-1}$, respectively in Becharof Lake and Ugashik Lake, whereas maximum ammonia levels never exceeded $30 \mu\text{g L}^{-1}$. Concentrations of reactive silicon were three times higher in Ugashik Lake compared to Becharof Lake. Chlorophyll *a* levels never exceeded $5 \mu\text{g L}^{-1}$ and averaged $<1 \mu\text{g L}^{-1}$ in both lakes. Seasonal changes in salient water chemistry and nutrient concentrations for each station by year for Becharof and Ugashik Lake are presented respectively, in Appendices C and D.

Results of ANOVA suggested there were spatial differences in water chemistry, nutrients, and chlorophyll *a* in Becharof Lake (Table 5). Post hoc (Tukey's pairwise comparisons) tests from ANOVA showed that Ruth Arm had significantly ($P<0.05$) lower conductivity, less alkalinity, and only half the concentration of the major cations calcium and magnesium than in the East Basin, West Basin, and Island Arm sampling stations. On the other hand, total phosphorus, total nitrogen, silicon, and chlorophyll *a* concentrations were twice as high ($P<0.05$) in Ruth Arm compared to the other three sampling sites. For Ugashik Lake, the ANOVA post hoc tests suggested concentrations of reactive silicon were higher ($P<0.05$) in the upper basin of Ugashik Lake (Stations C and D) compared to the lower basin (Stations A and B) (Table 6). However, for the most part ANOVA results suggested little or no station differences in other nutrients, water chemistry or chlorophyll *a* concentrations.

Lake Physical Characteristics

Excluding the Ruth Arm, median light extinction coefficient (K_d) in Becharof Lake varied from 0.126 to 0.209 m^{-1} , whereas the median euphotic zone depth (EZD) ranged from 22 to 37 m and the median Secchi disk (SD) transparency varied from 13.0 to 15.5 m (Figure 20a-c). Median K_d values were considerably higher and thus EZD and SD lower in shallow Ruth Arm (Station 3) compared to the other three sampling stations. In contrast, there were no obvious spatial differences in light regimes in Ugashik Lake (Figure 21a-c). Median K_d , EZD, and SD ranged from 0.193 to 0.217 m^{-1} , 21.3 to 24.2 m, and 7.0 to 9.3 m, respectively. During 1997-1999, neither lake stratified thermally during the open water periods, at least for any prolonged period. Instead, temperature decreased gradually ($<1^\circ \text{C}$) per meter of depth. Maximum water temperatures in the deeper basins of Becharof Lake reached approximately 12°C ; however, surface temperatures exceeded 15°C in Ruth Arm (Figure 22). In Ugashik Lake, maximum temperatures ranged from 12 - 13°C . Although some vertical heterogeneity with respect to water column temperature was apparent, there was no well-defined thermocline (Figure 23). However, in both lakes, thermal regimes varied considerably between years. In both lake, surface water (1 m) temperatures in mid-summer were 2 - 3°C warmer in 1997 and 2 - 3°C colder in 1999 compared to 1998 (Figures 24-25). Thus, inter-annual variability in thermal regimes appeared much greater than spatial differences.

Table 5. Least squares means from ANOVA to test for spatial (station) differences in general water chemistry, nutrients, and algal pigments for the 1-m depth in Becharof Lake, 1997-1999. Values that share the same letter do not differ significantly ($P > 0.05$; $df = 6$; Tukey pairwise).

Variable	Unit of measure	Station Mean			
		West (Sta. 1)	Island (Sta. 2)	Ruth (Sta. 3)	East (Sta. 4)
Conductivity	$\mu\text{mhos cm}^{-1}$	91 ^a	87 ^a	45 ^b	92 ^a
pH	Units	7.0 ^a	7.0 ^a	6.8 ^b	7.0 ^a
Alkalinity	mg L^{-1}	18.7 ^a	18.1 ^a	9.7 ^b	18.9 ^a
Turbidity	NTU	0.6 ^a	1.0 ^a	1.7 ^a	0.8 ^a
Color	Pt units	5.0 ^a	4.0 ^a	5.3 ^a	4.3 ^a
Calcium	mg L^{-1}	7.0 ^a	6.6 ^a	3.6 ^b	7.0 ^a
Magnesium	mg L^{-1}	1.9 ^a	1.8 ^a	0.6 ^b	1.9 ^a
Iron	$\mu\text{g L}^{-1}$	16 ^a	29 ^a	44 ^a	19 ^a
Total phosphorus	$\mu\text{g L}^{-1}$	3.0 ^a	4.2 ^a	9.6 ^b	3.6 ^a
Total filterable phosphorus	$\mu\text{g L}^{-1}$	2.5 ^{db}	4.1 ^{ab}	4.2 ^{cd}	2.0 ^{ad}
Filterable reactive phosphorus	$\mu\text{g L}^{-1}$	1.2 ^a	0.9 ^a	2.0 ^a	1.0 ^a
Kjeldahl nitrogen	$\mu\text{g L}^{-1}$	66 ^a	72 ^a	123 ^b	71 ^a
Ammonia	$\mu\text{g L}^{-1}$	10.8 ^a	8.5 ^a	9.3 ^a	11.7 ^a
Nitrate + nitrite	$\mu\text{g L}^{-1}$	11 ^a	10 ^a	24 ^a	12 ^a
Total nitrogen	$\mu\text{g L}^{-1}$	77 ^a	83 ^a	147 ^b	83 ^a
Reactive silicon	$\mu\text{g L}^{-1}$	266 ^a	529 ^a	1,389 ^b	296 ^a
Particulate organic carbon	$\mu\text{g L}^{-1}$	125 ^a	113 ^a	269 ^b	84 ^a
Chlorophyll <i>a</i>	$\mu\text{g L}^{-1}$	0.6 ^a	0.5 ^a	2.4 ^b	0.3 ^a
Phaeophytin	$\mu\text{g L}^{-1}$	0.3 ^a	0.3 ^a	0.9 ^a	0.1 ^a

Table 6. Least squares means from ANOVA to test spatial (station) differences in general water chemistry, nutrients, and algal pigments for the 1-m depth in the Ugashik lakes, 1997-1999. Values that share the same letter do not differ significantly ($P>0.05$; $df = 6$; Tukey pairwise).

Variable	Unit of measure	Station Mean			
		Lower Basin (Sta. A) (Sta. B)		Upper Basin (Sta. C) (Sta. D)	
Conductivity	$\mu\text{mhos cm}^{-1}$	56 ^a	56 ^a	62 ^b	65 ^c
pH	Units	7.0 ^a	7.0 ^a	7.1 ^{ac}	7.1 ^{bc}
Alkalinity	mg L^{-1}	14.7 ^a	14.7 ^a	17.2 ^b	17.6 ^b
Turbidity	NTU	0.6 ^a	0.9 ^b	0.7 ^a	0.7 ^a
Color	Pt units	5.0 ^a	5.0 ^a	5.0 ^a	4.0 ^a
Calcium	mg L^{-1}	3.5 ^a	3.6 ^{ac}	3.7 ^{bc}	3.7 ^b
Magnesium	mg L^{-1}	1.1 ^a	1.1 ^{ac}	1.2 ^{ac}	1.3 ^{bc}
Iron	$\mu\text{g L}^{-1}$	16 ^a	21 ^{ac}	19 ^{ac}	27 ^{bc}
Total phosphorus	$\mu\text{g L}^{-1}$	4.1 ^a	4.1 ^a	4.4 ^a	5.2 ^b
Total filterable phosphorus	$\mu\text{g L}^{-1}$	1.8 ^a	2.1 ^a	2.3 ^a	2.6 ^a
Filterable reactive phosphorus	$\mu\text{g L}^{-1}$	1.5 ^a	1.5 ^a	1.9 ^a	2.1 ^a
Kjelkahl nitrogen	$\mu\text{g L}^{-1}$	93 ^a	89 ^a	80 ^a	89 ^a
Ammonia	$\mu\text{g L}^{-1}$	8.3 ^a	11.0 ^a	8.9 ^a	8.1 ^a
Nitrate + nitrite	$\mu\text{g L}^{-1}$	19.8 ^{ab}	25.0 ^b	16.1 ^{bc}	12.5 ^{ac}
Total nitrogen	$\mu\text{g L}^{-1}$	113 ^a	114 ^a	96 ^a	101 ^a
Reactive silicon	$\mu\text{g L}^{-1}$	1,962 ^a	1,992 ^a	2,661 ^b	2,897 ^c
Particulate organic carbon	$\mu\text{g L}^{-1}$	95 ^a	94 ^a	91 ^a	118 ^a
Chlorophyll <i>a</i>	$\mu\text{g L}^{-1}$	0.41 ^a	0.42 ^a	0.35 ^a	0.41 ^a
Phaeophytin	$\mu\text{g L}^{-1}$	0.23 ^a	0.24 ^a	0.23 ^a	0.22 ^a

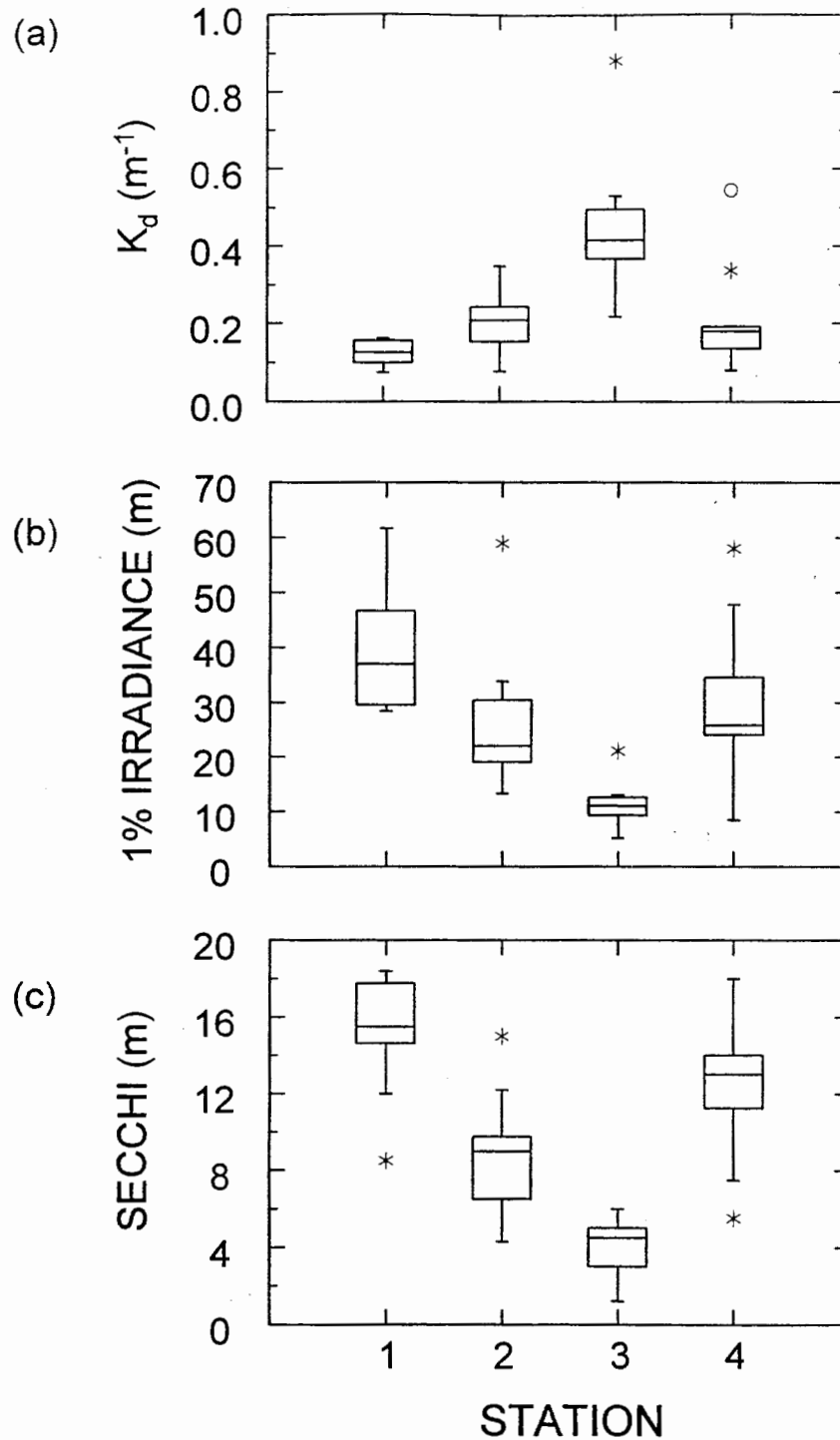


Figure 20. Box-plots of the (a) vertical light extinction coefficient (K_d), (b) depth of 1% light penetration, and (c) Secchi disk transparency by sampling station for Becharof Lake, 1997-1999. Values between 1.5 and 3 times the inter-quartile are plotted as asterisks. Values greater than 3 times the inter-quartile are plotted as circles.

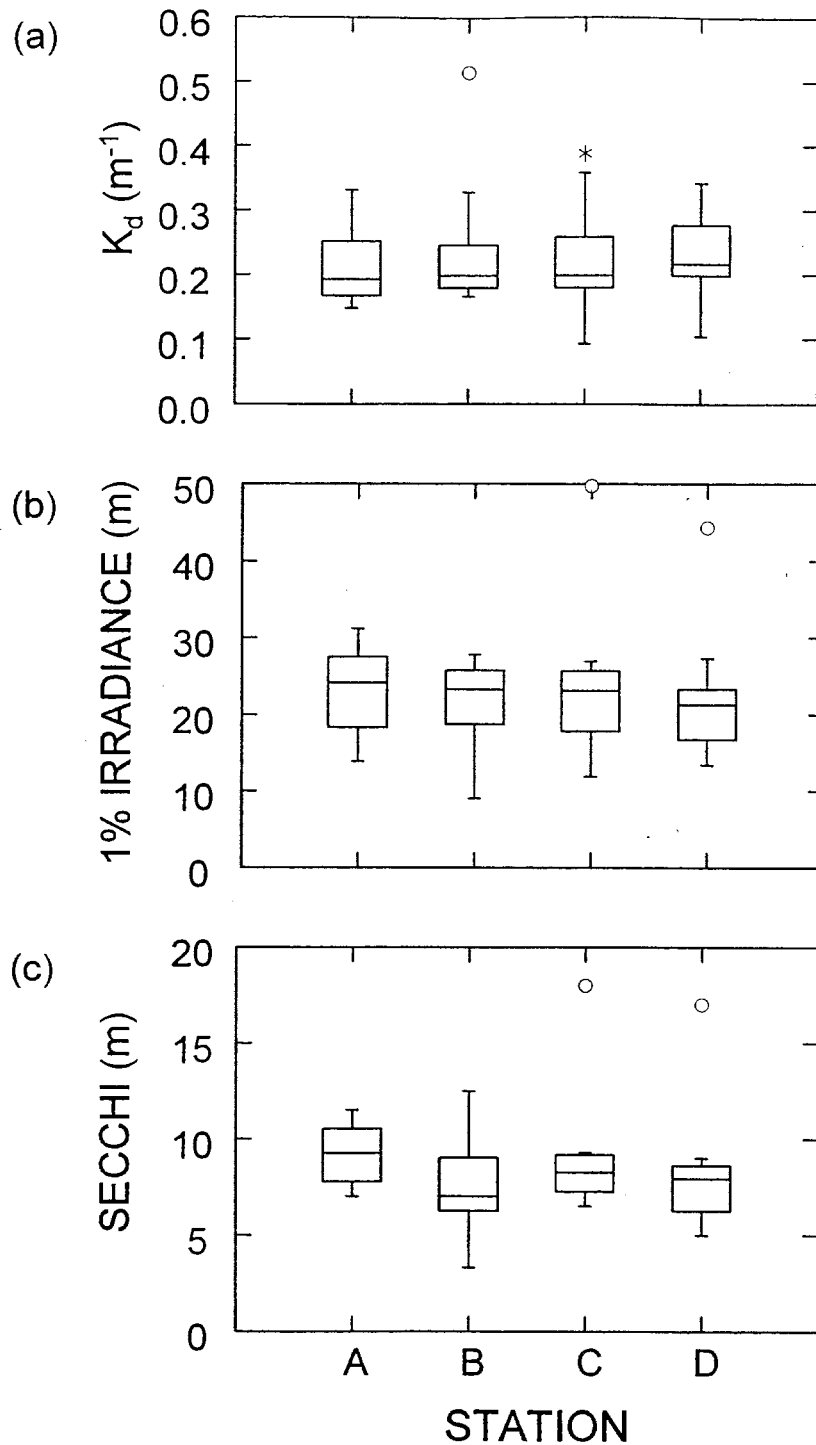


Figure 21. Box-plots of the (a) vertical light extinction coefficient (K_d), (b) depth of 1% light penetration, and (c) Secchi disk transparency by sampling station for the Ugashik lakes, 1997-1999. Values between 1.5 and 3 times the inter-quartile are plotted as asterisks. Values greater than 3 times the inter-quartile are plotted as circles.

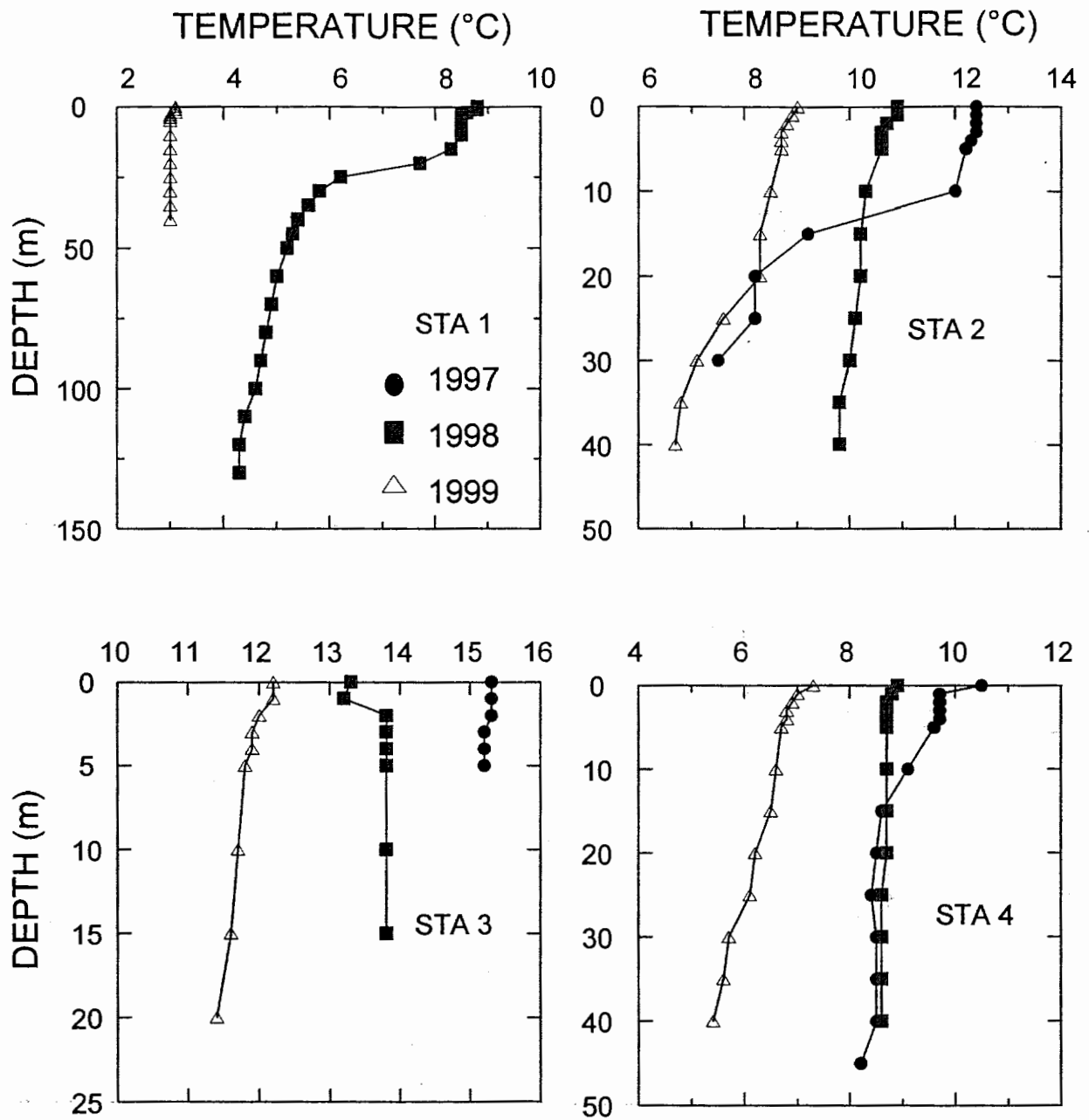


Figure 22. Vertical temperature profiles at four stations during time of maximum heat content (late July to early August) for Becharof Lake, 1997-1999.

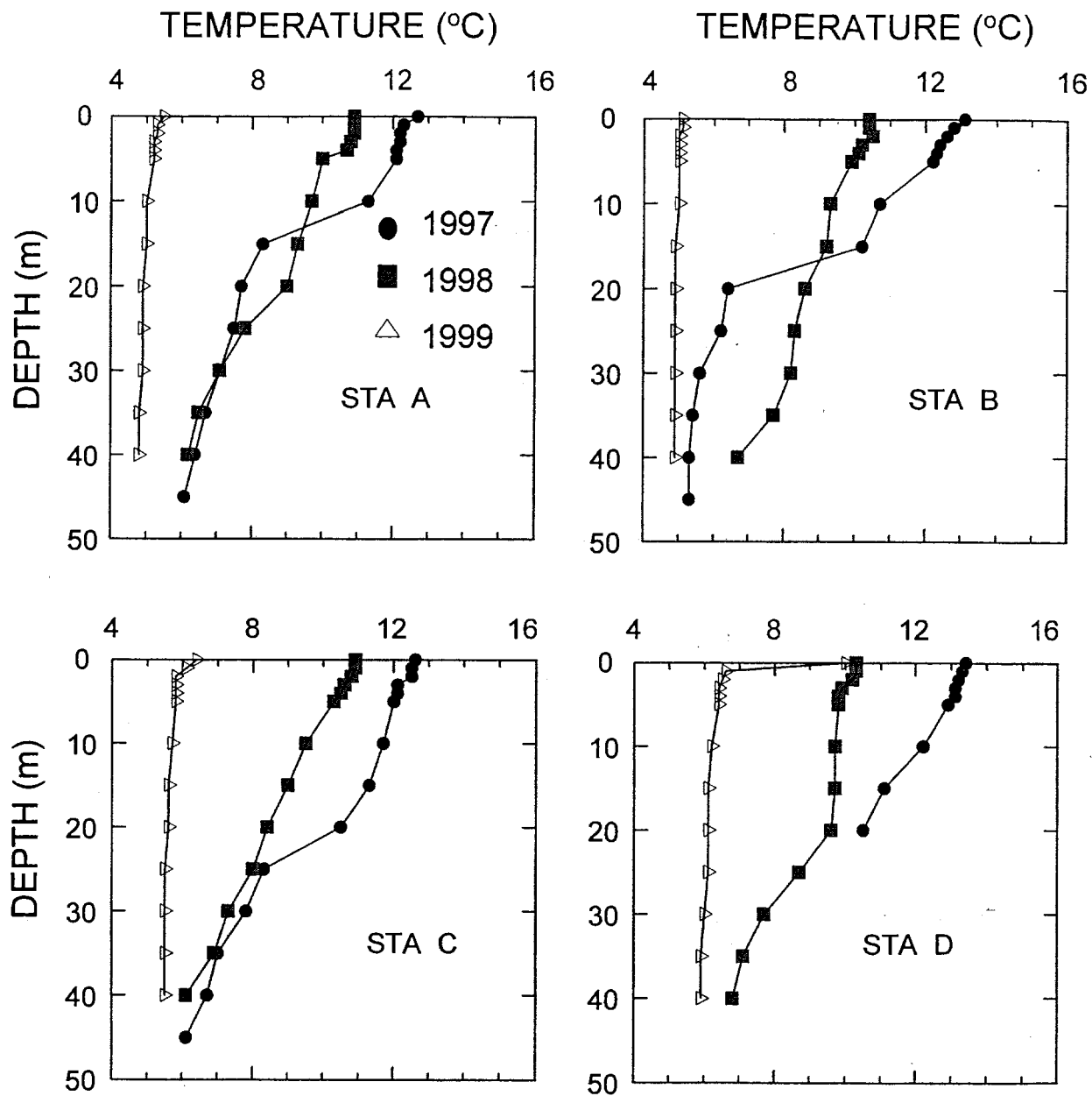


Figure 23. Vertical temperature profiles at four stations during time of maximum heat content (late July to early August) for the Ugashik lakes, 1997-1999.

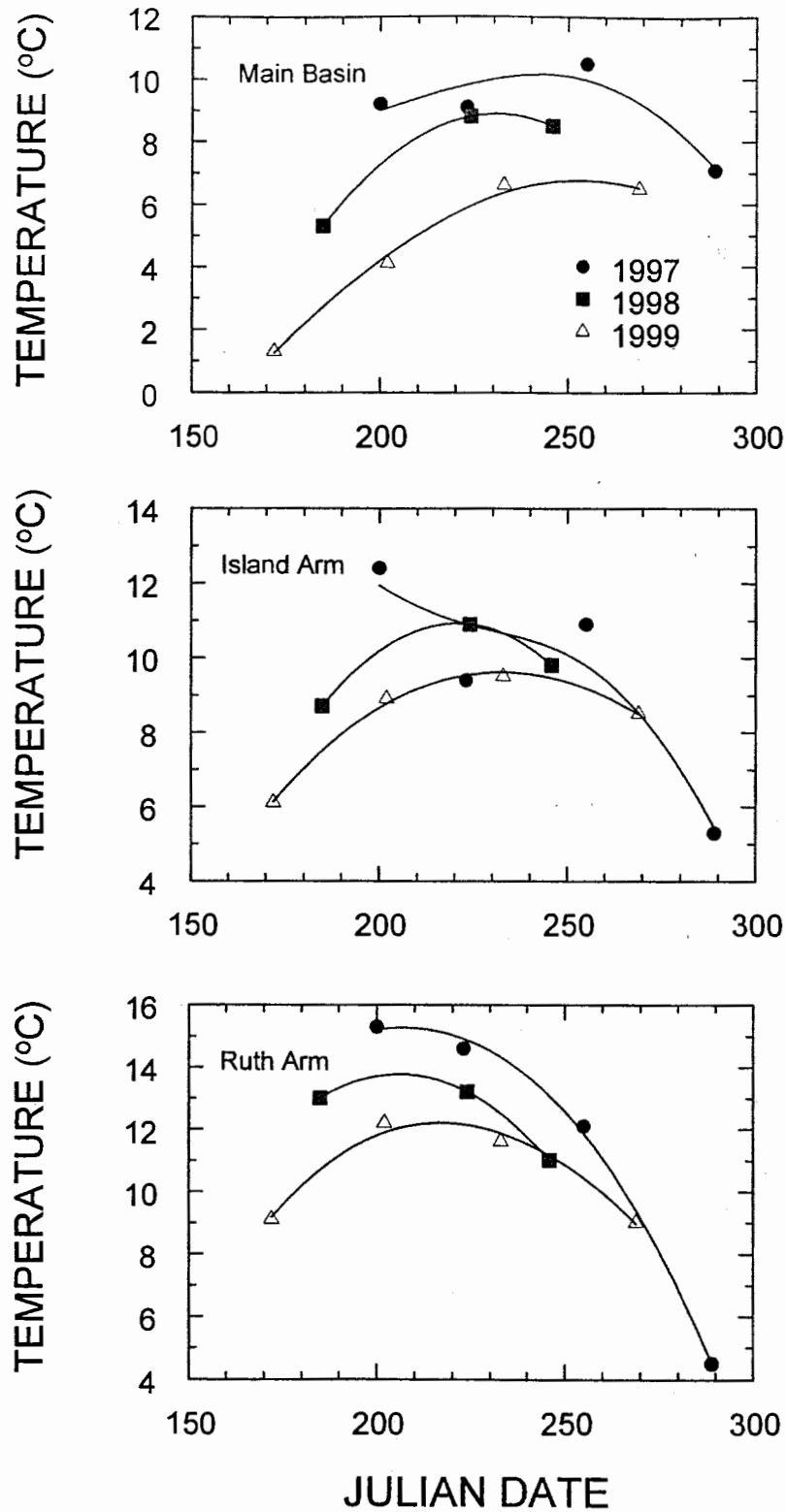


Figure 24. Seasonal changes in water temperatures of the 1-m stratum for three major basins in Becharof Lake, 1997-1999. A density-weighted least squares (DWLS) smoother was fitted to the data.

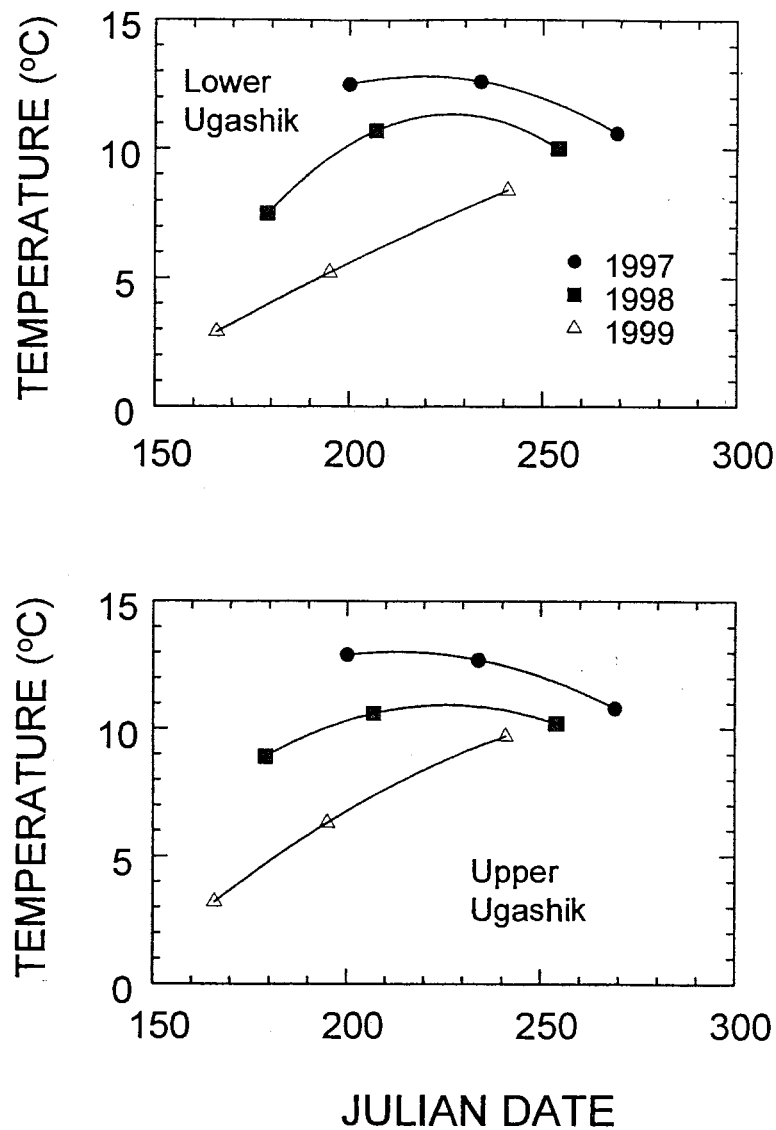


Figure 25. Seasonal changes in water temperatures of the 1-m stratum for two major basins in the Ugashik lakes, 1997-1999. A density-weighted least squares (DWLS) smoother was fitted to the data.

A useful time series of detailed water temperature data from Becharof and Ugashik lakes corresponding to sockeye escapement, smolt production, or adult return information does not exist. However, we examined annual terrestrial air temperatures for King Salmon, the nearest official climate-monitoring site to our two study lakes. Time series plots of monthly air temperature anomalies are presented in Figures 26-28. For the available years (1968-1999), a LOWESS fit suggested a warming trend began in the early 1980s and continued at least into the early 1990s. This is particularly evident in the time series of May, June and July air temperature anomalies. The increase was in the range of 1-1.5° C. On the other hand the LOWESS fitted data suggested that since the early 1990s, winter (December and January) air temperatures have perhaps decreased. There was no discernible trend in the temperature time series in the other months.

To assess the effect of air temperature on juvenile sockeye growth we generated a correlation matrix between age 1 smolt population characteristics (length, weight, and relative abundance) for both Egegik and Ugashik sockeye with monthly air temperature anomalies, assuming the summer months to be the most important (Table 7). There was little association between temperature and age 1 smolt size for either system as evidenced by the small correlation (r) coefficients. Bonferroni probabilities were not significant ($P=1.0$) for any of the coefficients. Although it appeared that there was a moderate positive association between the summer temperature anomalies and the proportion of age 1 smolts for the Egegik sockeye (r values ranged from 0.50-0.62), the correlations were not significant (P -values ranged from 0.91-1.0). From these data it appeared that there was little if any effect of summer air temperatures on smolt production, at least as indexed by the size and relative abundance of age 1 smolts. There was also no significant correlation between adult recruits-per-spawner and any of the summer temperature anomalies. However, we felt lagging the recruits-per-spawner data backward one year would better establish an association with lake thermal conditions and fry recruitment. That is, when lagged backward one year the recruits from a given brood year correspond to the air temperatures the subsequent rearing year. When the recruit-per-spawner data were lagged back one year the correlations between variables were all negative, though the correlations were not significant. The P -values between these variables ranged between 0.91 and 1.0.

DISCUSSION

Inferences on Stock and Recruitment in Relation to Smolt

For both Egegik and Ugashik sockeye salmon, there was an inability to derive clear compensatory stock-recruitment (S-R) relationships using all brood years (Cross et al. 1997; Figure 6). That is, there was no indication that higher escapements result in some limitation to the productivity (recruits-per-spawner) of these stocks. Instead, the number of adult recruits increased linearly as the parental escapement increased, though the variation about the regression lines was very large (Figure 7). However, considering only recent data, a significant Ricker model was derived for both Egegik ($P=0.05$; brood years

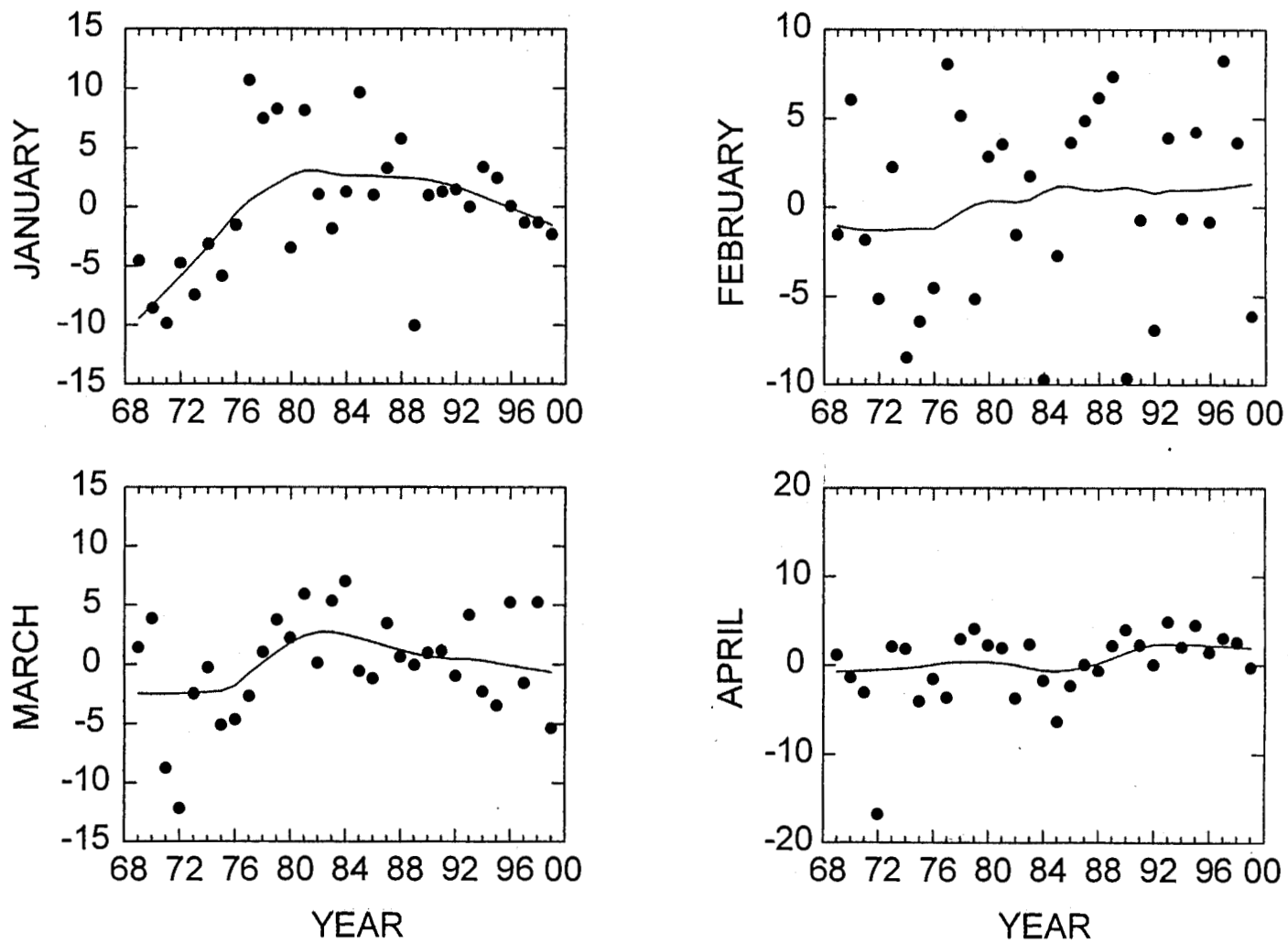


Figure 26. Monthly (January-April) air temperature ($^{\circ}\text{C}$) anomalies for King Salmon from 1969 to 1999, the solid lines are LOWESS fits to the data.

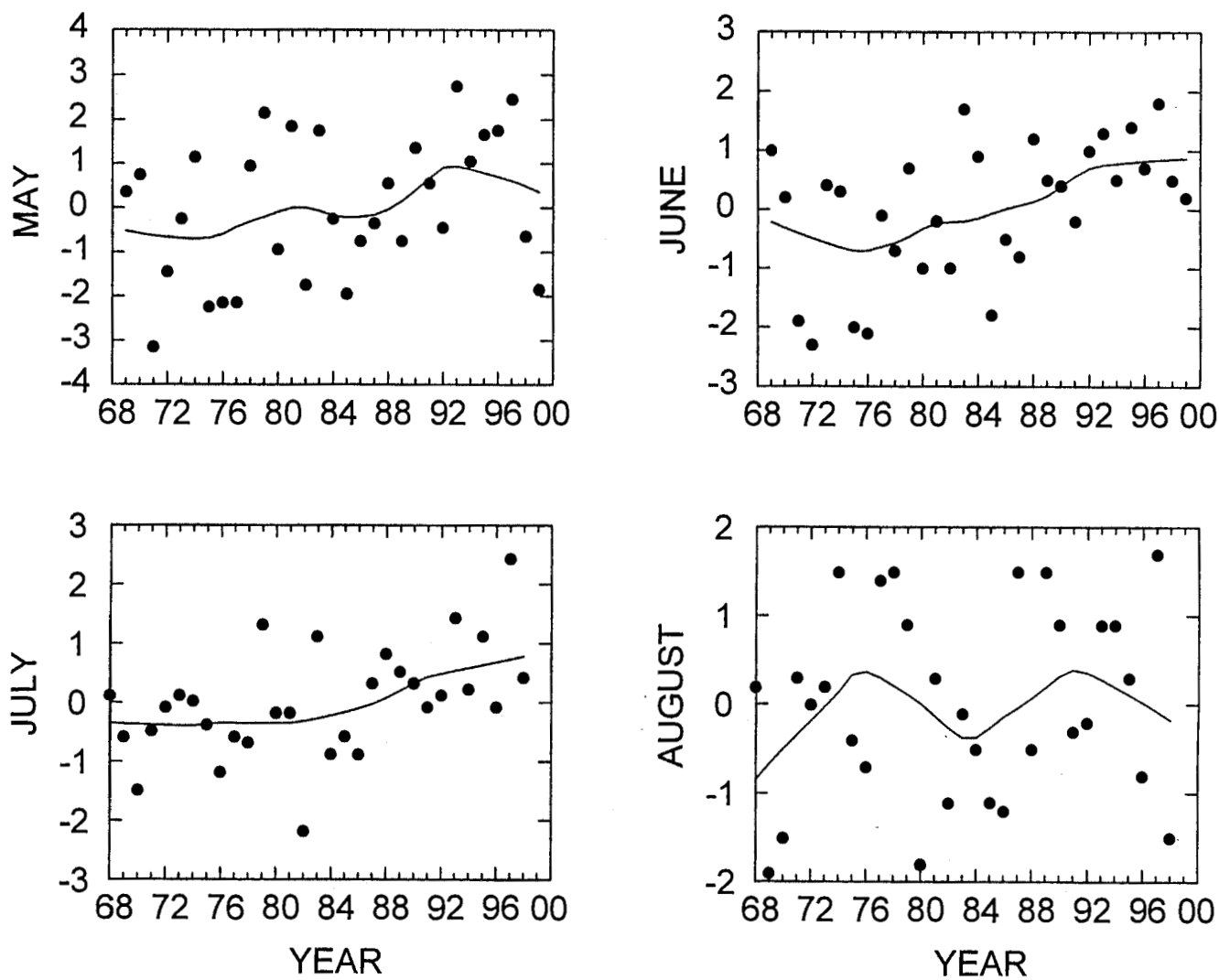


Figure 27. Monthly (May-August) air temperature (°C) anomalies for King Salmon from 1969 to 1999, the solid lines are LOWESS fits to the data.

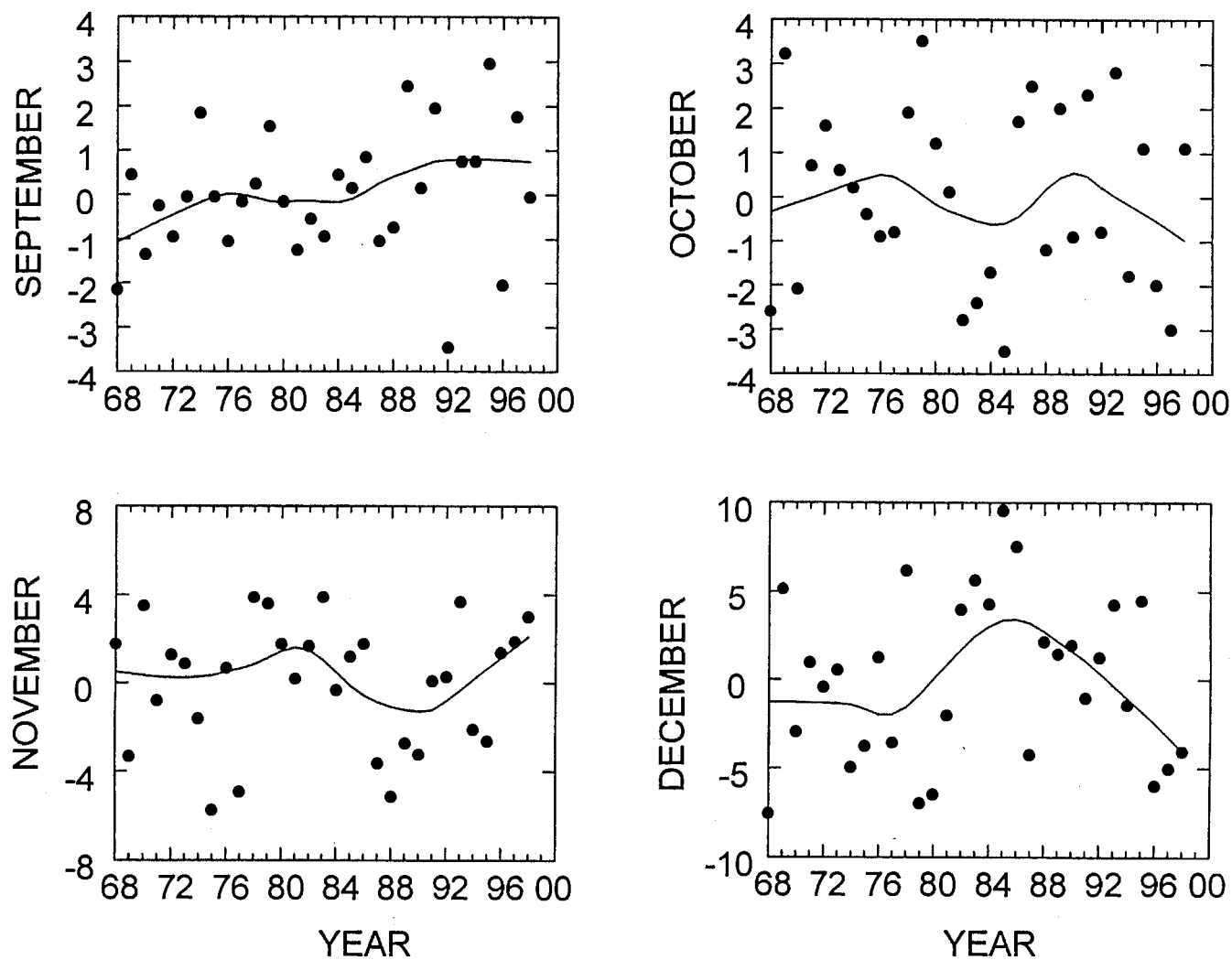


Figure 28. Monthly (September-December) air temperature ($^{\circ}\text{C}$) anomalies for King Salmon from 1969 to 1999, the solid lines are LOWESS fits to the data.

Table 7. Pearson's correlation (r) coefficients between age 1 smolt size, the relative abundance of age 1 smolts, adult recruits/spawner, and adult recruits/spawner lagged backward one year for Egegik and Ugashik sockeye versus summer (May, June, July, and August) monthly temperature anomalies. Monthly temperature anomalies are calculated as the difference between the 30 year (1969-1998) mean and the year specific average monthly temperature.

	May	June	July	August
Becharof Length (mm)	0.33	0.29	0.13	0.12
Weight (g)	-0.02	0.07	-0.04	-0.04
Relative Abundance (%)	0.62	0.50	0.59	0.60
Recruits/Spawner	-0.04	0.03	0.07	0.10
Lag (-1) Recruits/Spawner	-0.35	-0.31	-0.25	-0.21
Ugashik Length (mm)	0.16	0.39	0.09	-0.06
Weight (g)	0.14	0.45	-0.04	-0.17
Relative Abundance (%)	0.22	0.19	-0.05	-0.03
Recruits/Spawner	-0.09	-0.27	-0.17	0.40
Lag (-1) Recruits/Spawner	-0.49	-0.31	-0.16	-0.21

1976-1995) and Ugashik sockeye ($P=0.0003$; brood years 1974-1995) (Fair 2000). This may suggest non-stationarity of the S-R relationships and could present problems in determining escapement goal using compensatory models (Hilborn and Walters 1992). Nonetheless, assuming a density independent model best describes the S-R data for these two stocks, this observation is somewhat at odds with the lack of correlation between parental escapement and smolt production (Figures 11c, 12d). The latter would indicate some recruitment failure from the egg to fry or from the fry to smolt stage. Alternatively, the lack of correlation between the numbers of smolts produced as a function of parental escapement might also suggest a shortage of suitable spawning areas.

Under a scenario of limited spawning area, recruitment is proportional to the number of spawners until the spawning habitat is fully utilized (seeded). After which there is no further recruitment with additional escapement. Presumably this is because of superimposition on the redds, or increased egg mortality from crowding (Foerster 1968). To our knowledge, estimates of potential spawning areas for the Becharof and Ugashik systems have not been cataloged so it is difficult to determine whether the amount of spawning habitat is substantially smaller on a relative basis to other systems in the surrounding Bristol Bay area. However, Burgner et al. (1969) documented that escapement per unit of nursery lake area (spawner density) was lower in both Egegik and Ugashik lakes compared with many other sockeye systems in southwest Alaska. In addition, observations via aerial and foot surveys by ADF&G reveal that many Becharof Lake spawners are concentrated within the smaller Island Arm and Ruth Arm basins. Assuming the Egegik and Ugashik systems are spawning area limited, we would expect the adult recruits-per-spawner values to be relatively constant up to a point followed by a decline as additional spawners do not contribute to recruitment. However, this pattern was not evident in the S-R data. The regression slopes of \ln recruits-per-spawner against the number of spawners were not significantly different from zero (Figure 6). All that we can determine now is that adult returns for the Egegik and Ugashik systems are positively related to the total number of smolts produced (Figure 14a, 14c) and that the recruitment from smolt to adult decreases somewhat with increasing smolt numbers (Figure 14b, 14d). We cannot determine the optimum escapement to maximize smolt output because the curve is nearly linear. Thus, the interpretation of the effects of the size of the spawning stock on subsequent adult recruitment (Figure 7) is probably not a practical predictive tool.

Inferences on Stock and Recruitment in Relation to the Forage Base

It is possible that the relationship between the number of sockeye smolts and parental escapement are partially masked by year-to-year variations in freshwater-rearing conditions. There are many examples of effects of environmental variability, intraspecific competition, and predation that influence freshwater growth and survival of sockeye salmon (e.g., Foerster 1968; Burgner 1987). Studies have suggested that growth and survival of sockeye salmon in lakes is closely tied to hydrometeorological conditions (Selifonov 1987), euphotic volume (Koenings and Burkett 1987), primary production (Reimann and Meyers 1992), and zooplankton biomass (Hyatt and Stockner 1985;

Koenings and Kyle 1997). Competition between adjacent year classes of sockeye juveniles for available forage may also underlie the cyclic pattern in adult returns in some systems (Schmidt et al. 1995).

Our limnological studies span too short a time to permit direct comparisons between variability in freshwater conditions (e.g., zooplankton) and indices of smolt production. Nonetheless, for Becharof Lake, Martin and Lloyd (1996) derived a positive linear relationship between the total numbers of smolts produced in one year versus the relative abundance of age 2 smolts (holdovers) in the subsequent year. Such a relationship is an indication of density dependent effects i.e., a grazing interaction between adjacent year classes of fry. We repeated their analysis with the addition of more recent data (Figure 13b). Although the relationship was still significant, the r^2 value was smaller with most of the variation (74%) unexplained. As for Ugashik sockeye, no such relationship between smolt production and subsequent proportion of holdovers existed at all. In addition, if density dependent effects were occurring in the pelagic zone, we would expect that the size of smolts to vary inversely to some degree with smolt abundance (an index of fry density). Although correlations between smolt size and the number of smolts produced were negative, the strength of the correlations was weak (Figure 17) and the correlations were not significant. Thus, proxy indicators of zooplankton dynamics and sockeye planktivory in relation to smolt demographics did not provide compelling evidence of a grazing effect in Becharof and Ugashik lakes.

If we still accept the hypothesis that intense competition for food resources (planktivory) is limiting juvenile sockeye production, we would also expect to see a reduced number of large-bodied cladocerans (Brooks and Dodson 1965; Goodlad et al. 1974; Kyle et al. 1988) in these lakes as escapements increase. On the other hand, total abundance and biomass of the zooplankton may not change substantially. Rather, high grazing pressure results in a shift toward smaller size distributions of zooplankton (see Northcote 1988 for review). Unfortunately, data are unavailable to compile a reasonably long time series of zooplankton populations in Becharof and Ugashik lakes for comparisons with smolt and adult sockeye abundances. Nonetheless, average total macrozooplankton densities and biomass in both Becharof and Ugashik lakes were quite high compared with other nursery lakes in Alaska (see Edmundson et al. 1992; Table 3). Moreover, the recent (1997-1999) mean body sizes of the major zooplankton taxa are not necessarily reflective of intense size selective predation. Both lakes contained populations of large-bodied *Diaptomus* sp. zooplankters (Table 2), a copepod which often disappears quickly under high stocking densities or high levels of escapement (Edmundson et al. 1993; Koenings and Kyle 1997). In Becharof and Ugashik lakes, the calanoids, which were for the most part *Diaptomus* sp., composed most of the total macrozooplankton biomass (Figure 19).

Because abundant populations of planktivorous fish tend to reduce the number of large-bodied zooplankton, particularly large (>1 mm) *Daphnia* spp. (Mazumder et al. 1990; Mazumder and Lean 1994), we further considered the possibility of a density-dependent mechanism at work in Becharof and Ugashik lakes. Although we found a paucity of cyclopoids and calanoids in terms of both density (Appendix Figures A5-A6) and biomass (Appendix Figures 8-9) in Ruth Arm of Becharof Lake compared to the other

stations, cladoceran densities were higher (Appendix Figure A7). In addition, under high zooplanktivory, phytoplankton can be released from consumer control (*see* Carpenter and Kitchell 1993 for review of trophic cascades). Indeed, chlorophyll (an index of algal biomass) concentrations were three times higher in Ruth Arm compared to the other stations (Table 5; Appendix Figure C5). Yet, higher algal biomass may also be a function of increased nutrient loading (Vollenweider 1968). In addition, shallow lakes (or basins) tend to have higher productivity than deeper lakes. Thus, the shallow Ruth Arm basin may act to concentrate nutrients or promote internal phosphorus loading (Fee 1979). The cladoceran dominated zooplankton community structure in Ruth Arm may simply result from their competitive advantage over copepods under more eutrophic conditions rather than grazing effects. Furthermore, the mean size of *Daphnia* spp. was fairly consistent across all stations (Appendix Figures A3-A4). This suggests that sockeye planktivory is no more severe in Ruth Arm than in the other lake areas. Even though there may be more spawners in the Island Arm and Ruth Arm basins, we are not yet convinced that there is a spatial "bottle neck" in juvenile sockeye growth and survival relative to the forage base in Becharof Lake. Nonetheless, it is difficult to determine if the differences in zooplankton community structure in Ruth Arm are the result of top-down or bottom-up forces.

Small-bodied cladocerans such as *Bosmina* sp. were conspicuously absent from Ugashik Lake (Mathisen et al. 1998; Table 2), which might be inferred as evidence of intense sockeye planktivory. Yet, a macrozooplankton species composition dominated by small-bodied *Bosmina* spp. was a result of intense zooplanktivory in Frazer Lake (Kodiak Island) (Kyle et al. 1988). In the case of sockeye salmon juveniles, their gill rakers cannot retain particles (zooplankton) having a mean diameter less than about 0.4 mm (Koenings et al. 1985). A mean body size of *Bosmina* spp. of about 0.3 to 0.5 mm is common in Alaskan sockeye nursery lakes under a wide range of spawner densities (J. M. Edmundson, ADF&G, Soldotna, personal communication). While we cannot determine the cause for a lack of cladoceran populations in Ugashik Lake, several recent studies have suggested that the stoichiometry of sestonic nitrogen to phosphorus ratios and phosphorus to carbon ratios in pelagic systems may place food quality constraints on zooplankton herbivores (Hessen 1993; Hassett et al. 1997; Sterner et al. 1998). That is, high particulate nitrogen to phosphorus ratios tend to favor more calanoids, whereas low ratios support higher densities of daphnids. Further research is needed (e.g., particulate nutrient analysis) to assess whether the seston elemental stoichiometry influences the demographics of the zooplankton community in Ugashik Lake. At this time, the complete lack of cladoceran populations in this lake remains an enigma to us.

Despite the potential for greater fry recruitment (i.e., higher spawner density) in Ugashik Lake and increased grazing pressure, recent (1997-1999) mean macrozooplankton standing stock (biomass) was higher in Ugashik Lake than Becharof Lake (Figure 19; Table 3). Nonetheless, we felt comparing our grazing pressure index values with other sockeye lakes might provide further inferences about whether Becharof Lake and Ugashik Lake are more food resource limited relative to a shortage of suitable spawning areas (recruitment limitations). Among a dozen lakes the index of grazing pressure was by far the lowest in Becharof and Ugashik lakes (Table 3). It is worth noting that

Eshamy Lake was considered to be a spawning area limited system (Koenings and Kyle 1997) and it had one of the lowest grazing pressure index values (7.0) among this data set. On the other hand, escapements in excess of the carrying capacity have been suggested as a cause for the decline in productivity (adult recruit-per-spawner) for both Coghill Lake (Edmundson et al. 1992) and Crescent Lake (J. A. Edmundson, ADF&G, Soldotna, personal communication) in southcentral Alaska. In these lakes the grazing pressure index values averaged about 80 and 90, respectively. Thus, we do not believe the large size of smolts coupled with high levels of zooplankton biomass, and low spawner densities supports the contention of a strong grazer effect in Becharof or Ugashik lakes.

Inferences on Stock and Recruitment in Relation to Temperature

Growth of juvenile sockeye salmon is also influenced by temperature (Brett 1971). Under warmer temperatures and longer growing season, juveniles tend to grow faster and may achieve some threshold size to migrate more as age 1 smolts (Selifonov 1987). Thus, climate changes may mask the relationship between the number of smolts and parental escapement (Figure 11c and 12c). With their broad exposure to the ocean climate and frequent strong winds (Figure 1), thermal stratification does not develop in Becharof Lake (Figure 22) or Ugashik Lake (Figure 23). The result is that coastal lakes such as these have longer growing (ice-free) seasons than lakes further from the influence of oceanic climate (LaPerriere 1997). Although Mathisen et al. (1998) suggested that during the 1970s, warmer climatic conditions produced warmer water temperatures, longer growing seasons, and increased primary production in Becharof and Ugashik lakes. On the other hand, lakes situated further inland in the Bristol Bay region did not experience similar oceanic influences over the same time period. Mathisen et al. (1998) suggested that this is a partial cause for the significant increases in sockeye salmon production that occurred for the Egegik and Ugashik systems relative to other Bristol Bay sockeye stocks. However, neither detailed water temperature data nor measurements of primary productivity in the nursery lakes were presented in that analysis. Relating growth or smolt size and year-to-year fluctuations in lake temperatures requires a more detailed annual assessment of thermal regimes and distributions of sockeye juveniles over the course of the season (Edmundson and Mazumder 2000a). Except for the last few years (Figures 22-25), these data are not available for Becharof and Ugashik lakes.

To assess the temperature hypothesis, we examined terrestrial air temperature data from the nearby town of King Salmon over the past 30 years. Because of the close correlation between surface water temperatures and air temperatures, the latter are often used as a proxy for lake thermal conditions (Shuter et al. 1980). Examination of the monthly air temperature anomalies for the summer showed a period of warming during the 1970s and early 1980s (Figure 27), which was in agreement with the observations of Mathisen et al. (1998). However, we found no significant correlation between sockeye smolt size or age composition with respect to air temperature nor was temperature correlated with the number of recruits-per-spawner (Table 7). While we do not discount a strong influence of temperature on the growth of juvenile sockeye salmon (Burgner 1987; Edmundson and

Mazumder 2000b), it did not help to explain the decline in the number of smolts-per-spawner (Figure 11b and 12b) nor the decoupling between smolt abundance and parental escapements (Figure 11d and 12d) in Becharof and Ugashik lakes.

Inferences on Stock and Recruitment in Relation to Predators

There has also been some recent debate among fishery managers and researchers about the influence of predators on juvenile sockeye abundance in these two lakes. Mathisen et al. (1997) suggested predation by Arctic char (*Salvelinus alpinus*) and Arctic grayling (*Thymallus arcticus*) on juvenile sockeye salmon was the primary cause of the recent decline in smolt abundance for the Ugashik system. However, his conclusion was largely inferred from trophic levels estimated from stable nitrogen isotope ratios of smolt and predator fish taken from nearby Becharof Lake. Subsequent to that study, Mathisen and Sands (1999) took a rather novel approach in assessing sockeye salmon dynamics. They examined stable nitrogen isotope data from various biota in conjunction with the development of a steady-state ecosystem (ECOPATH) model (Christensen and Pauley 1992) to determine trophic levels and relationships between species in Becharof Lake. They concluded that sockeye production in Becharof Lake was to a large extent under predator (e.g., Dolly Varden [*Salvelinus malma*]) control. It should be noted that many assumptions are necessary in generating trophic transfer coefficients in these kinds of models. That is, consumption values are often obtained from the literature for the same or similar species rather than on direct empirical evidence of diet composition. Nonetheless, the stable isotope analysis in the Mathisen and Sands (1999) study helps to corroborate the results of their ecosystem model.

Our knowledge of predators in these nursery lakes is scanty. We cannot determine the role of predators on sockeye salmon dynamics because we have no information on predator growth rates or population abundances in the Egegik and Ugashik systems. However, if we accept the hypothesis that apex predators heavily influence smolt production (Mathisen and Sands 1999) then we might expect smolt abundance to oscillate in response to the magnitude of the predator populations. That is, a build-up of predators would seemingly follow, at some time lag, years of high fry recruitment until a negative feedback from intense piscivory resulted in a subsequent decline in predator abundance (e.g., see Carpenter and Kitchell 1993 for review of trophic cascade). There does appear to be some cycling in smolt abundances with respect to brood year, at least in Becharof Lake (Figure 11a), even though smolt production is largely independent of spawner abundance (Figure 11c). This lends some credence to the predator control hypothesis. However, further study is necessary to make generalizations about the capacity of these two systems to produce smolt in relation to predators. While a census of predator populations is problematic and expensive in lakes of this size, it may be important for management of these stocks to collect representative scale or otolith samples to index predator abundance. That is, a predator influence might emerge from examining their age structure and growth increments in comparison with varying escapement levels or smolt abundances.

Conclusions and Recommendations

In the final consideration of spawning area limitations, food supply, temperature, and predators, we believe it is the lack of suitable spawning area that limits sockeye production in the Egegik and Ugashik systems. There are no functional relationships between the number of spawners and subsequent smolt output (Figures 11c, 12c). The numbers of spawners per square kilometer of lake area in Becharof and Ugashik lakes contrasts sharply with that of other lakes (Table 3). Sockeye planktivory (density-dependent effects) seemed very low, as reflected from zooplankton species composition (Table 2) densities (Figure 18), biomass (Figure 19), and from our grazing pressure index (Table 3). In addition, the mean sizes of sockeye smolts were fairly large (Figures 15a, 16a) and sizes were not strongly related to smolt abundance (Figure 17). Furthermore, air temperature fluctuations did not summarize the variation in the mean smolt size nor did it strongly influence the age composition of smolts (Table 7). There is indirect evidence that runs of juvenile sockeye may be subjected to predator control, at least in Becharof Lake (Mathisen and Sands 1999). However, the number of juvenile sockeye eaten by predators and its relation to the number of smolts produced per spawner and the apparent decline in smolt production is not fully understood. Thus, it is difficult to determine the optimum spawning escapement relative to maximum returns or yield of sockeye salmon for the Egegik and Ugashik systems.

While our estimate of spawners to maximize yield involved a rather "rough and ready" approach, the temporal trends in S-R data (Figures 5a-c), tabular summary of escapements and resultant yields (Table 1), and graphical portrayal of the Markov data for each of the stocks (Figures 8a-b) produced similar estimates of optimum escapements. For Becharof Lake, optimum escapements seemed to be in the range of 1.0 million to 1.5 million spawners, while for Ugashik the number of spawners to maximize yield was between 600,000 and 900,000 sockeye. We recommend the upper end of the ranges for both systems largely because these levels correspond to the point where the number of adult recruits from parental escapement begins to show large variability (Figure 7a-b). Below these levels, adult recruits were roughly proportional to the number of spawners. These estimates of optimum escapement were very similar to the current escapement goals for the Egegik and Ugashik systems (Cross et al. 1997).

In conclusion, our analysis may help to relieve some of the uncertainty surrounding the biological escapement goals for the Egegik and Ugashik sockeye stocks. In addition, our analysis shows how even a short time series of limnological data can complement S-R information in assessing escapement goals. Nonetheless, we encourage development of a longer time series of limnological data sets in these important and large-sized nursery lakes. Furthermore, paleolimnological analysis of lake sediment cores has the capability to assess lake conditions over a long time series, well before commercial exploitation and in modern times under different management schemes (Finney 1998). Such an approach was recently applied to the Karluk Lake sockeye salmon resulting in a convincing recommendation for revising the existing escapement goal (Schmidt et al. 1998). Paleolimnological studies are currently underway in Becharof and Ugashik lakes as part

of a cooperative study involving U.S. Fish and Wildlife Service, University of Alaska Fairbanks, and Alaska Department of Fish and Game. Integration of these data with S-R information may provide further insights into the population dynamics of the Egegik and Ugashik sockeye salmon. Finally, we strongly support the collection of ecological data from all aspects of the life phases of sockeye salmon as the best way to help to disentangle the total mortality across the nursery lake and ocean components. It is a trophodynamic approach that will lead to improvements in fishery resource conservation and the ability to forecast future fish stocks.

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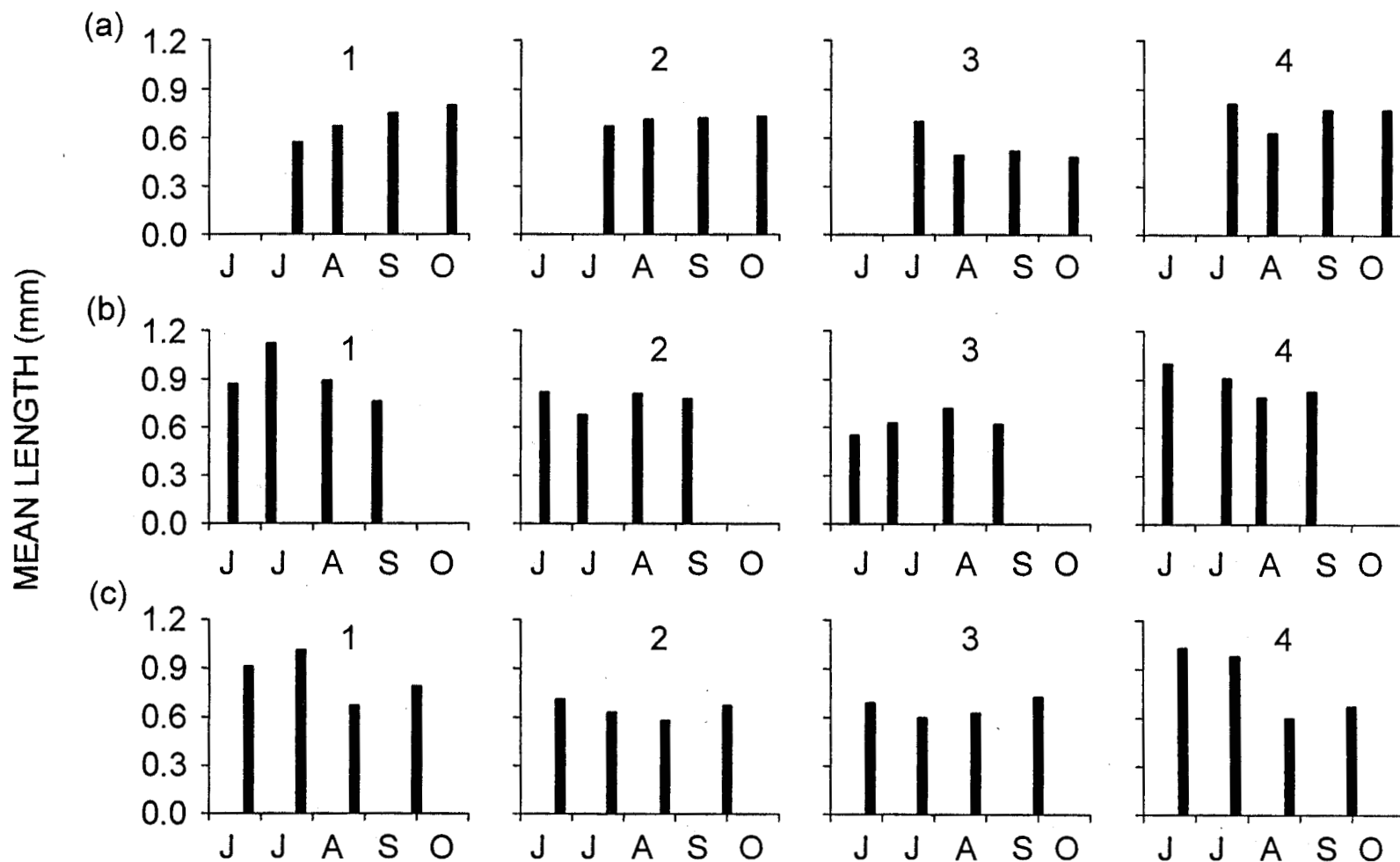
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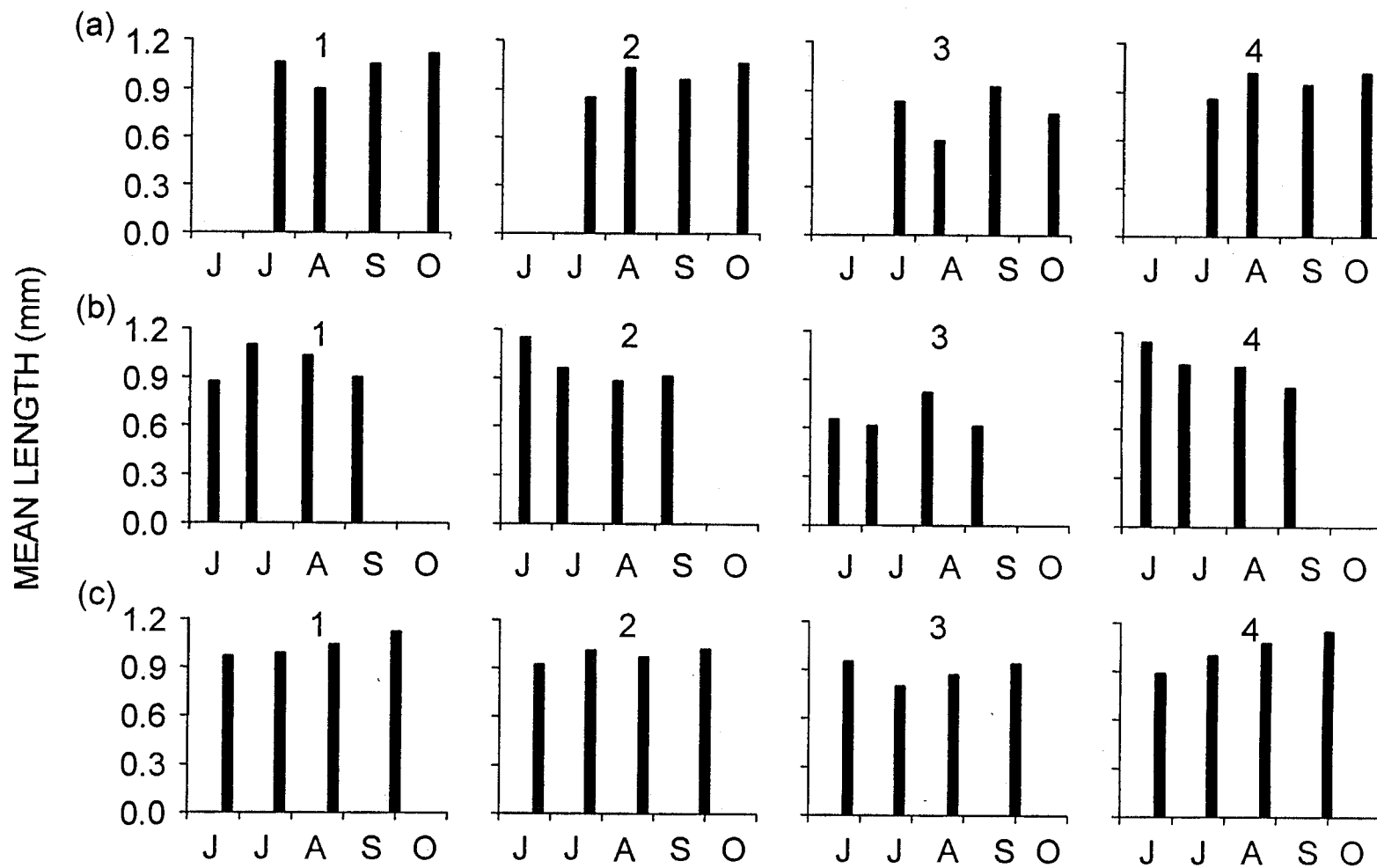
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APPENDIX A

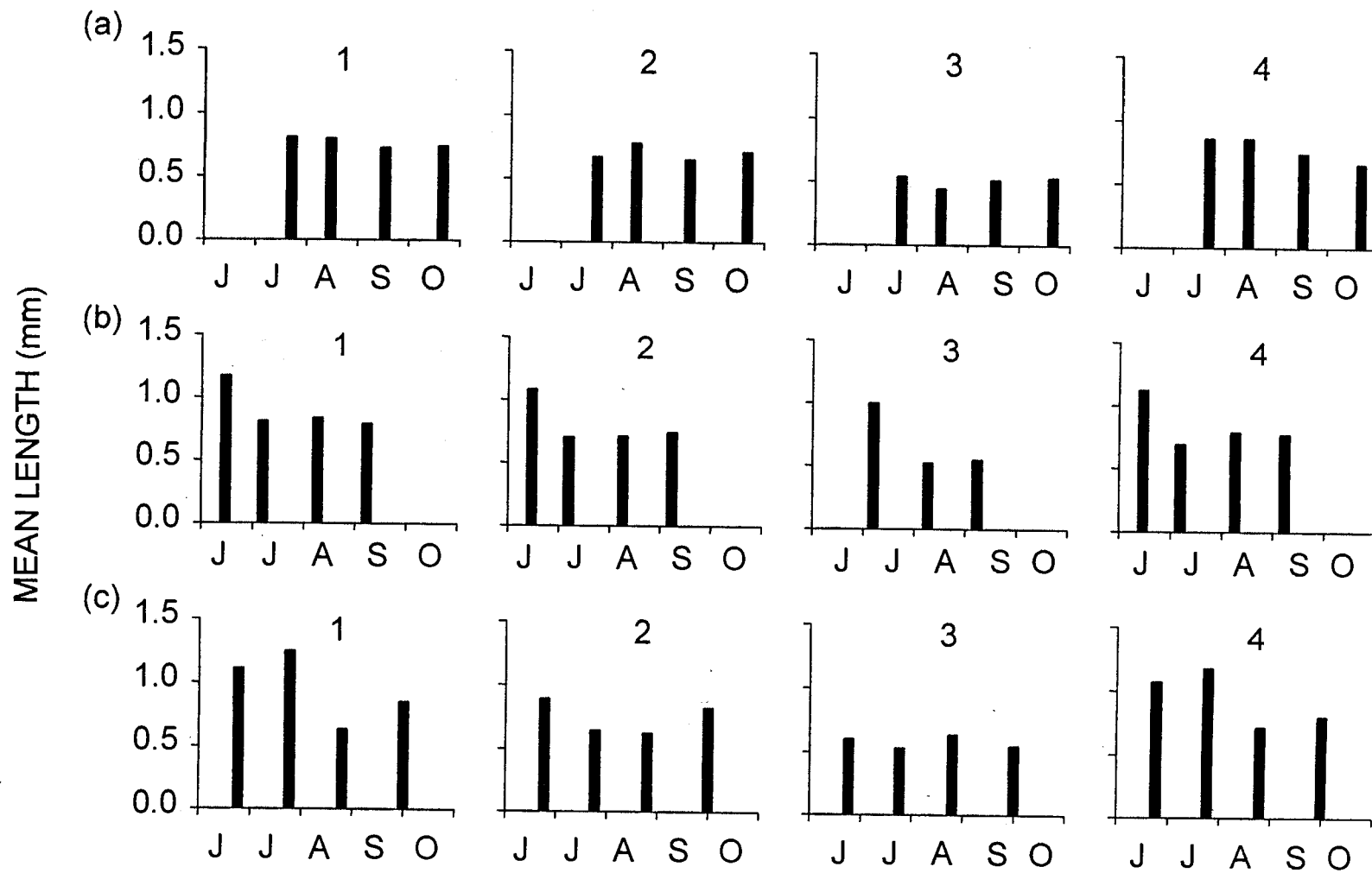
Seasonal Changes in Macrozooplankton Mean Body Size, Density, and Biomass by Major Taxonomic Group In Becharof Lake, 1997-1999



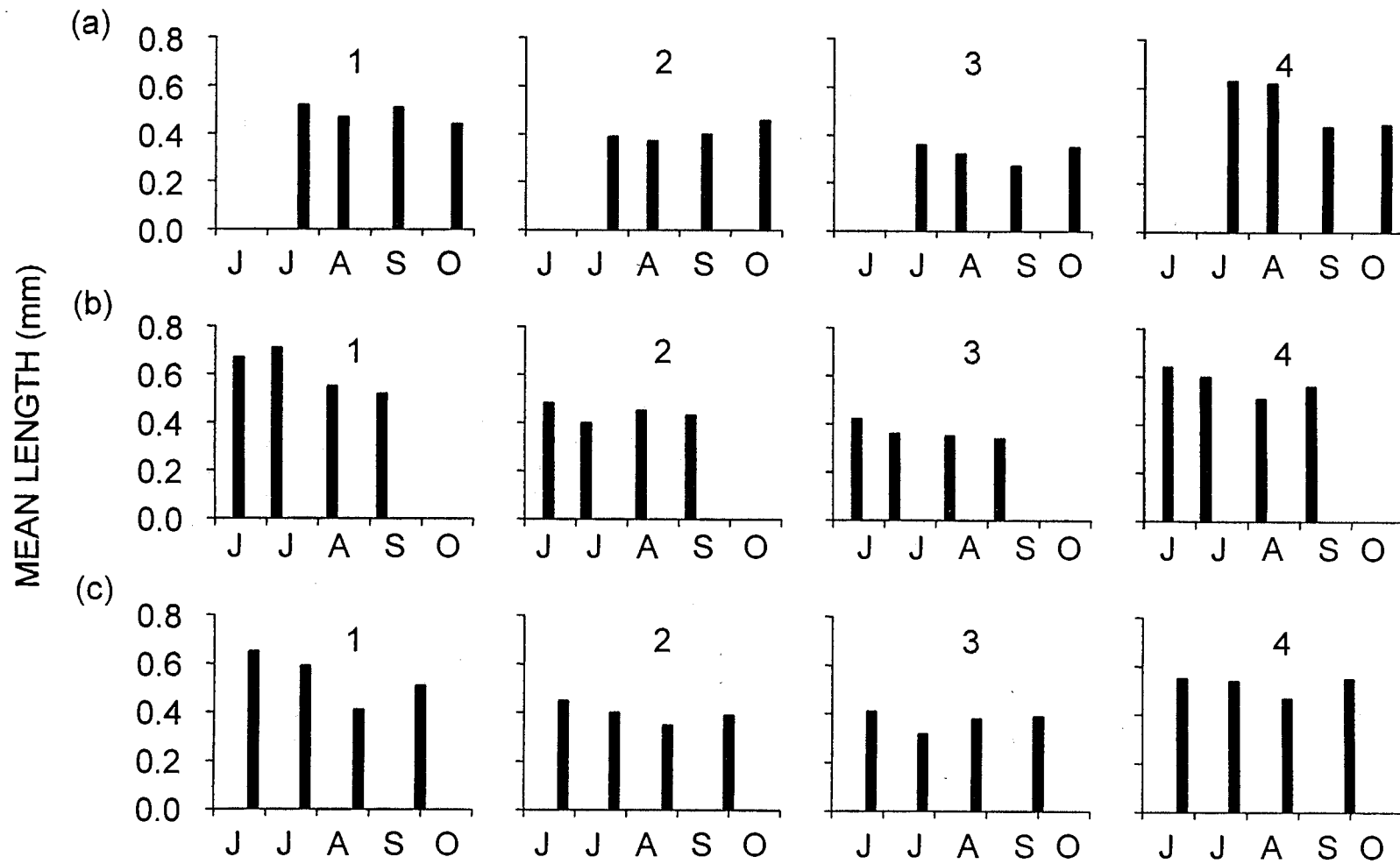
Appendix A.1. Seasonal changes in mean body length of cyclopoids at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



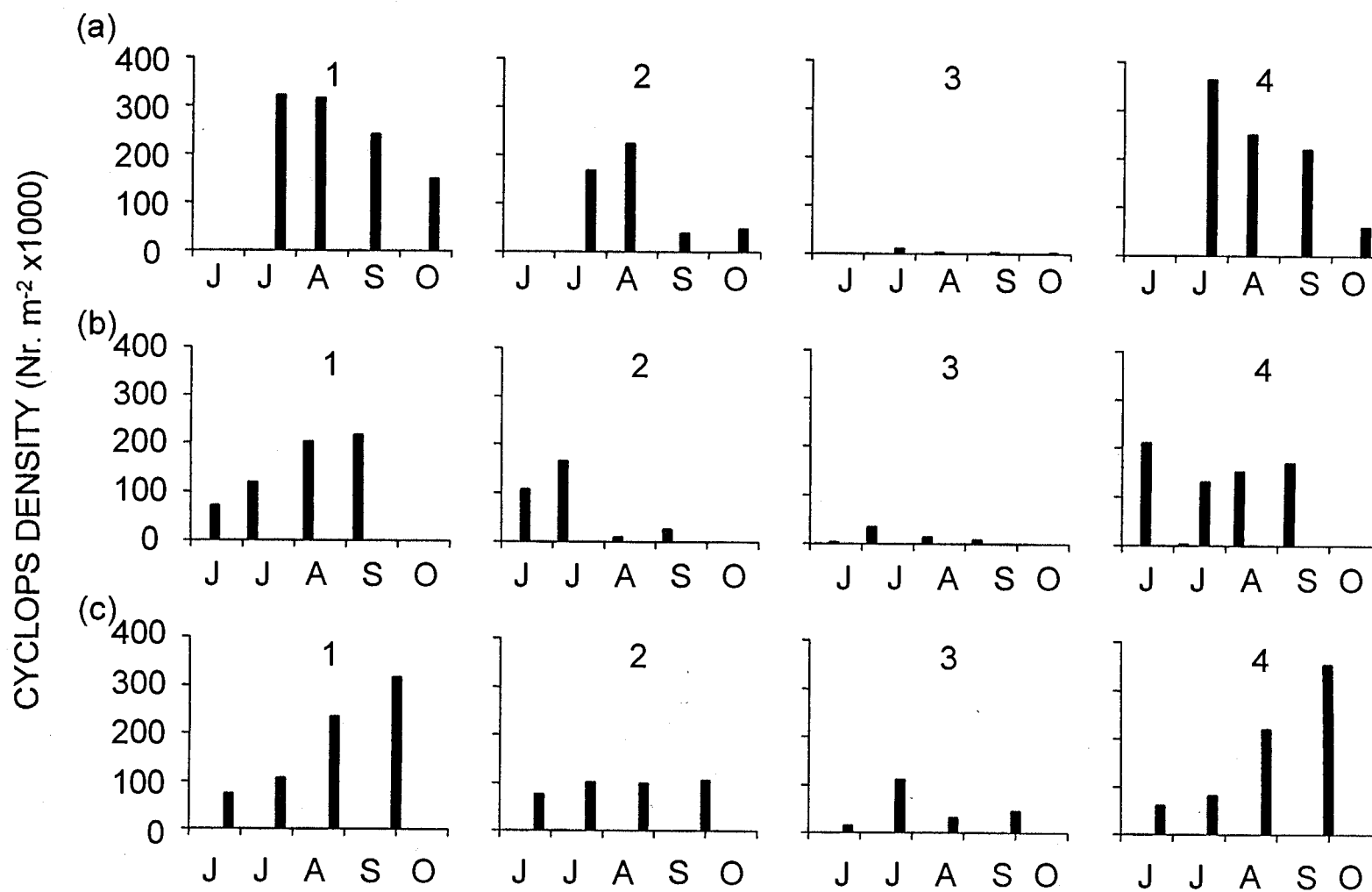
Appendix A.2. Seasonal changes in mean body length of *Diaptomus* spp. at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



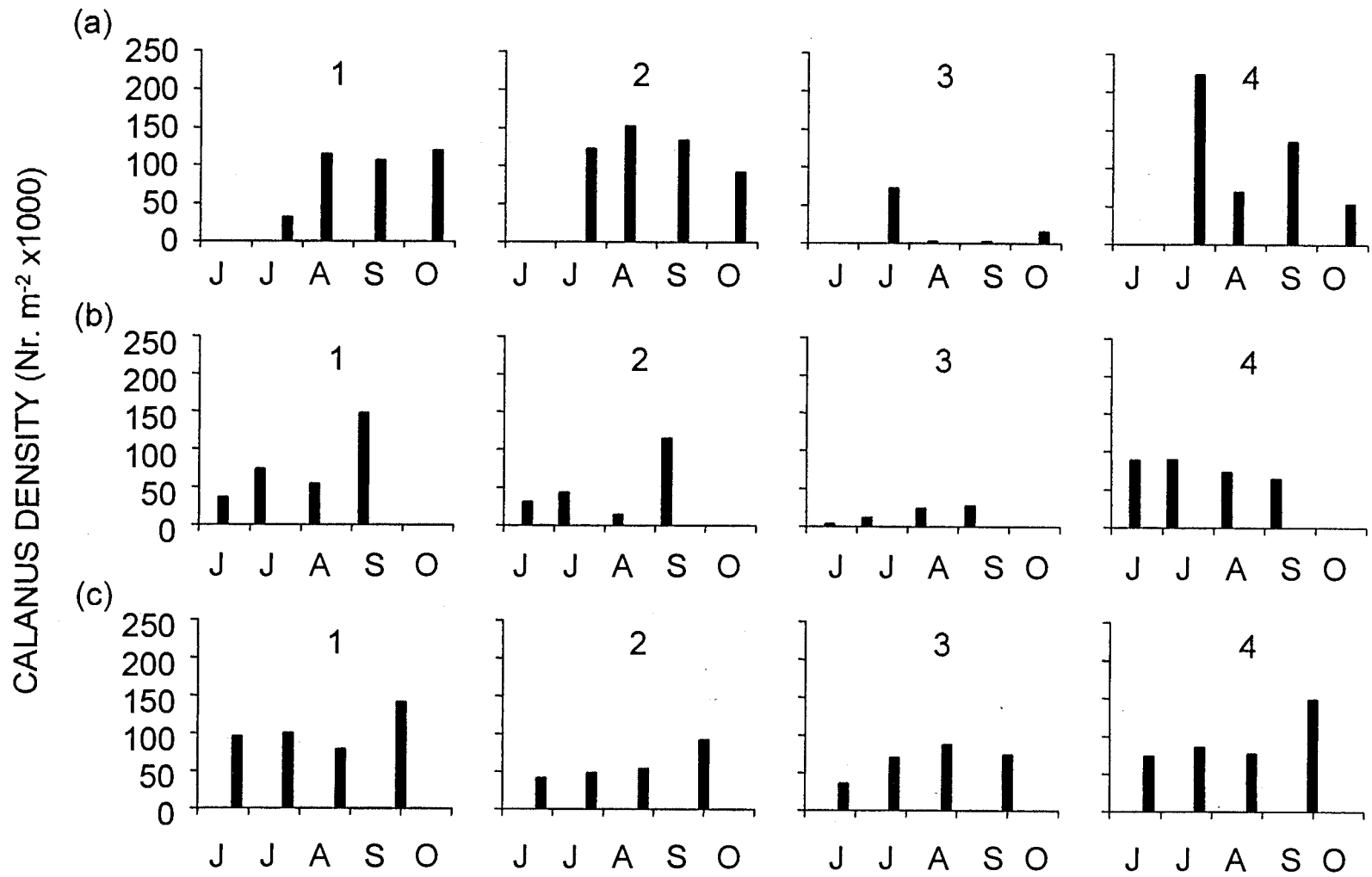
Appendix A.3. Seasonal changes in mean body length of daphnids at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



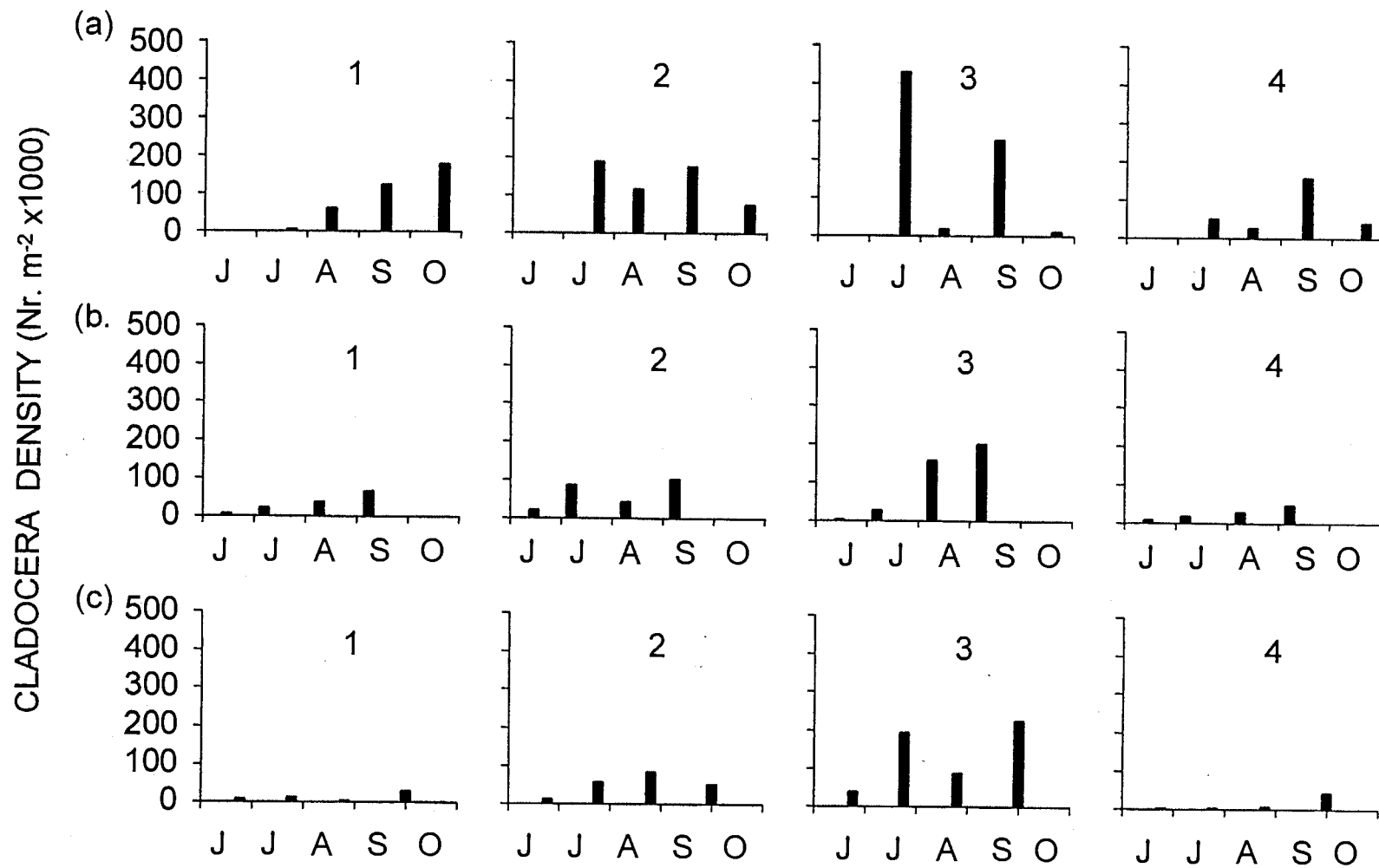
Appendix A.4. Seasonal changes in mean body length of bosminids at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



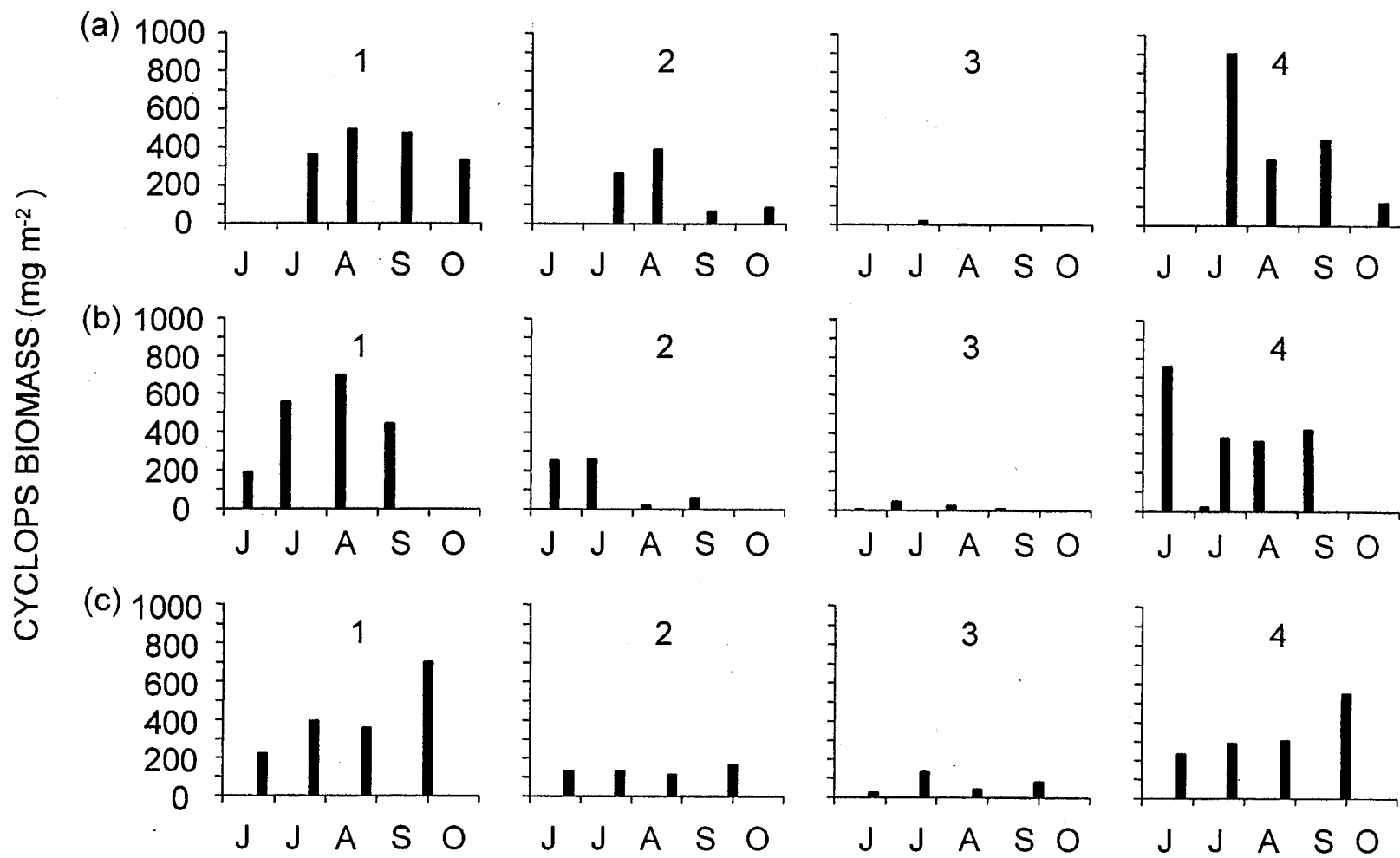
Appendix A.5. Seasonal changes in cyclopoid density at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



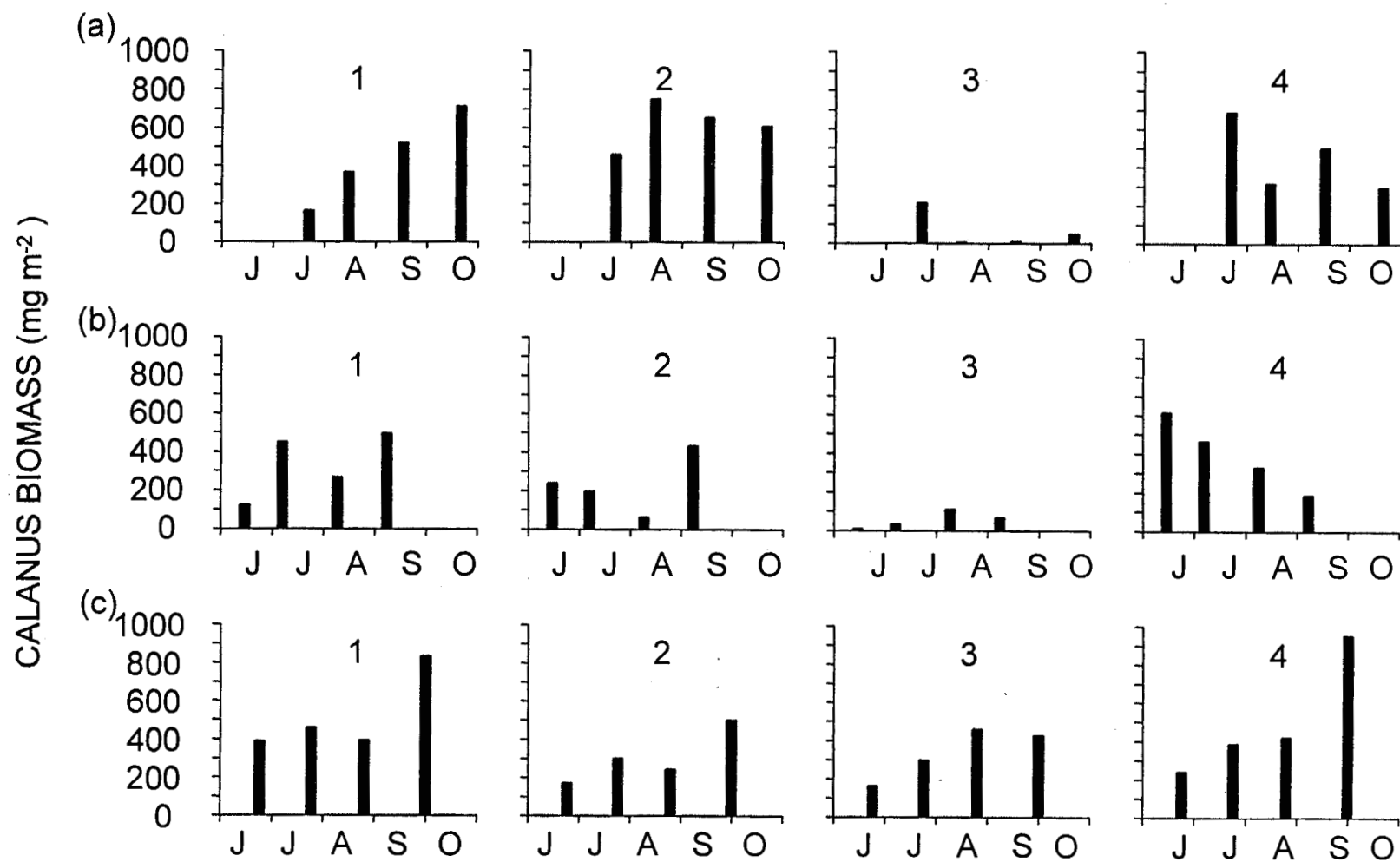
Appendix A.6. Seasonal changes in calanoid density at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



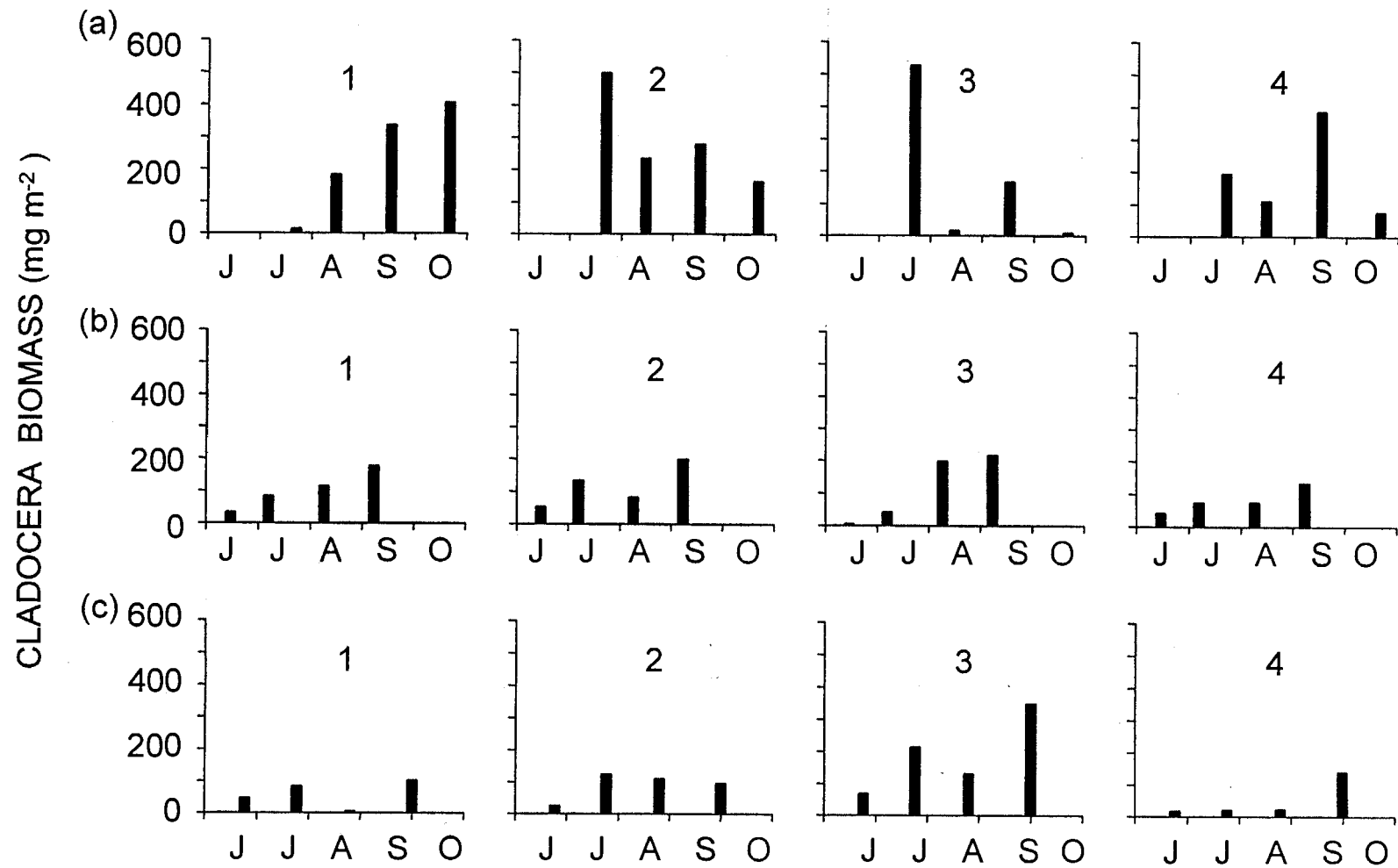
Appendix A.7. Seasonal changes in cladoceran density at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



Appendix A.8. Seasonal changes in cyclopoid biomass at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



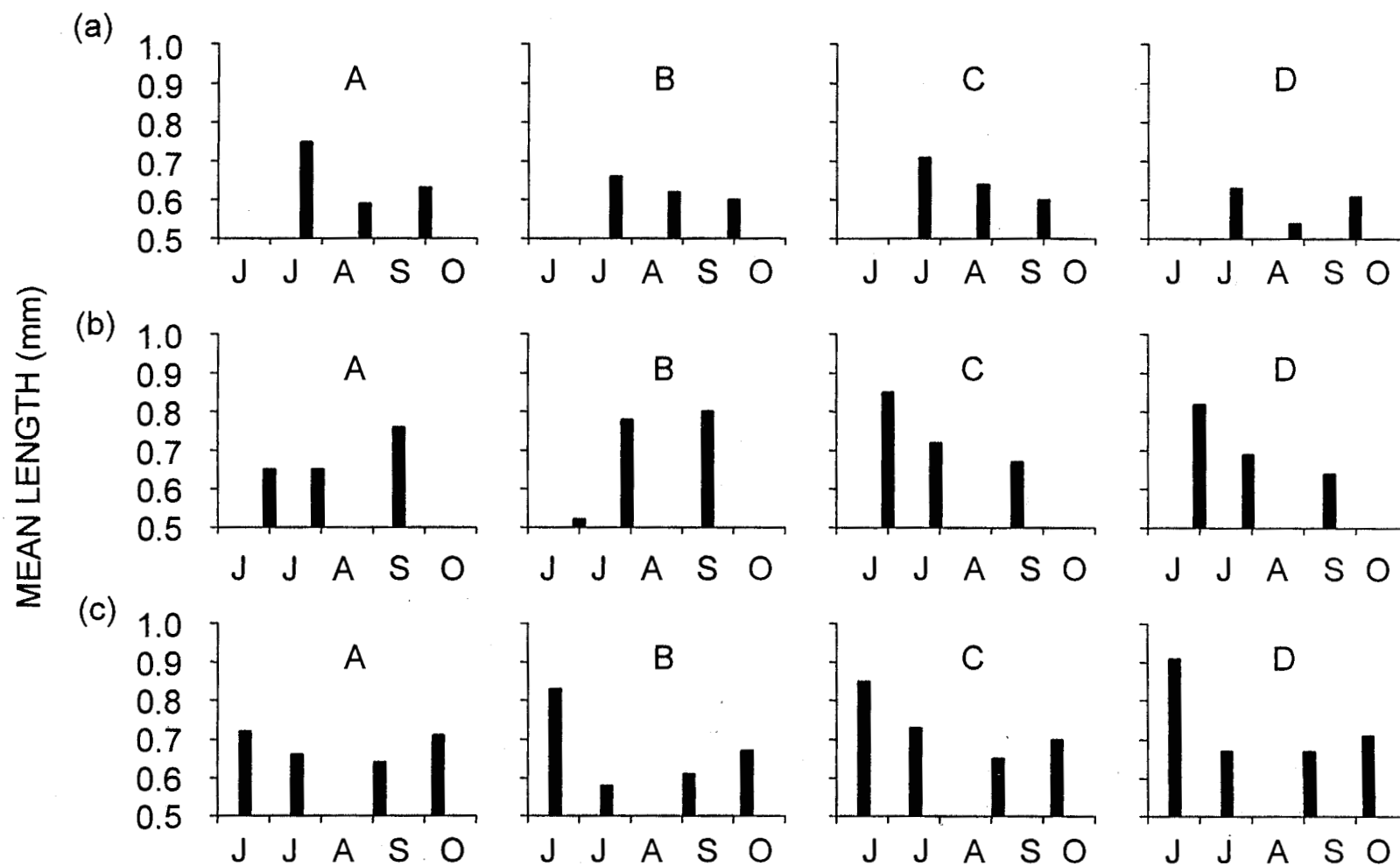
Appendix A.9. Seasonal changes in calanoid biomass at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



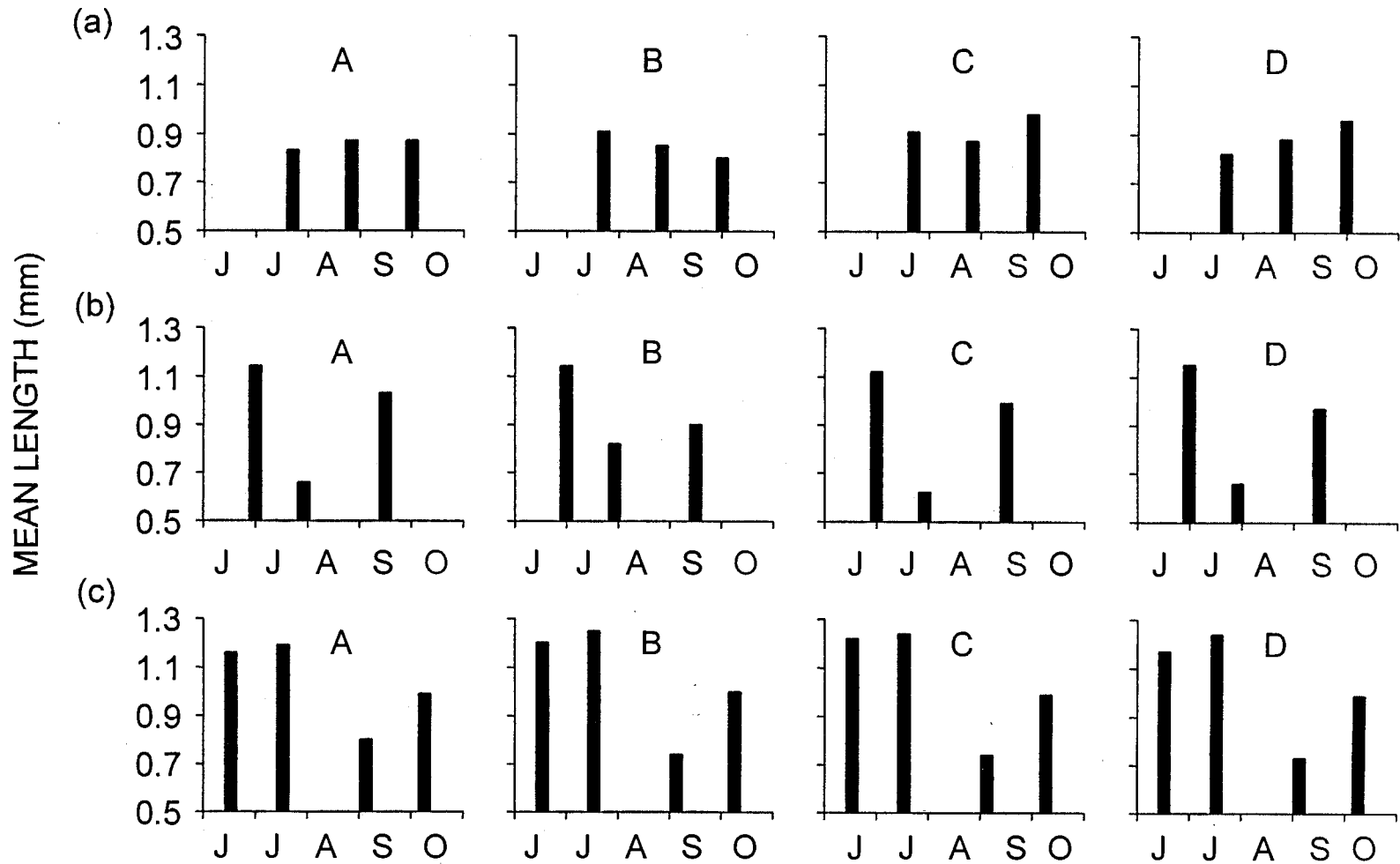
Appendix A.10. Seasonal changes in cladoceran biomass at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.

APPENDIX B

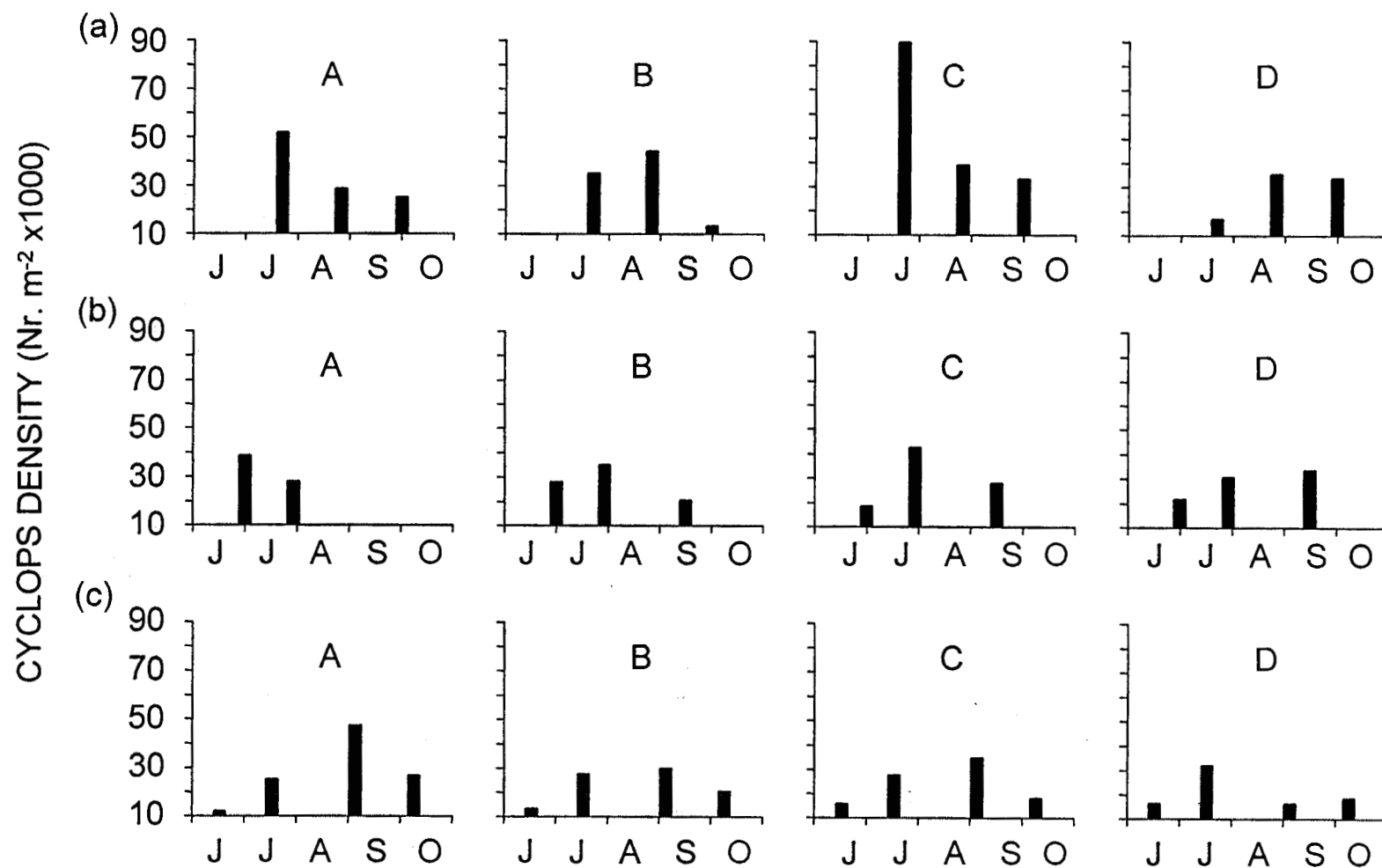
Seasonal Changes in Macrozooplankton Mean Body Size, Density, and Biomass by Major Taxonomic Group in the Ugashik Lakes, 1997-1999



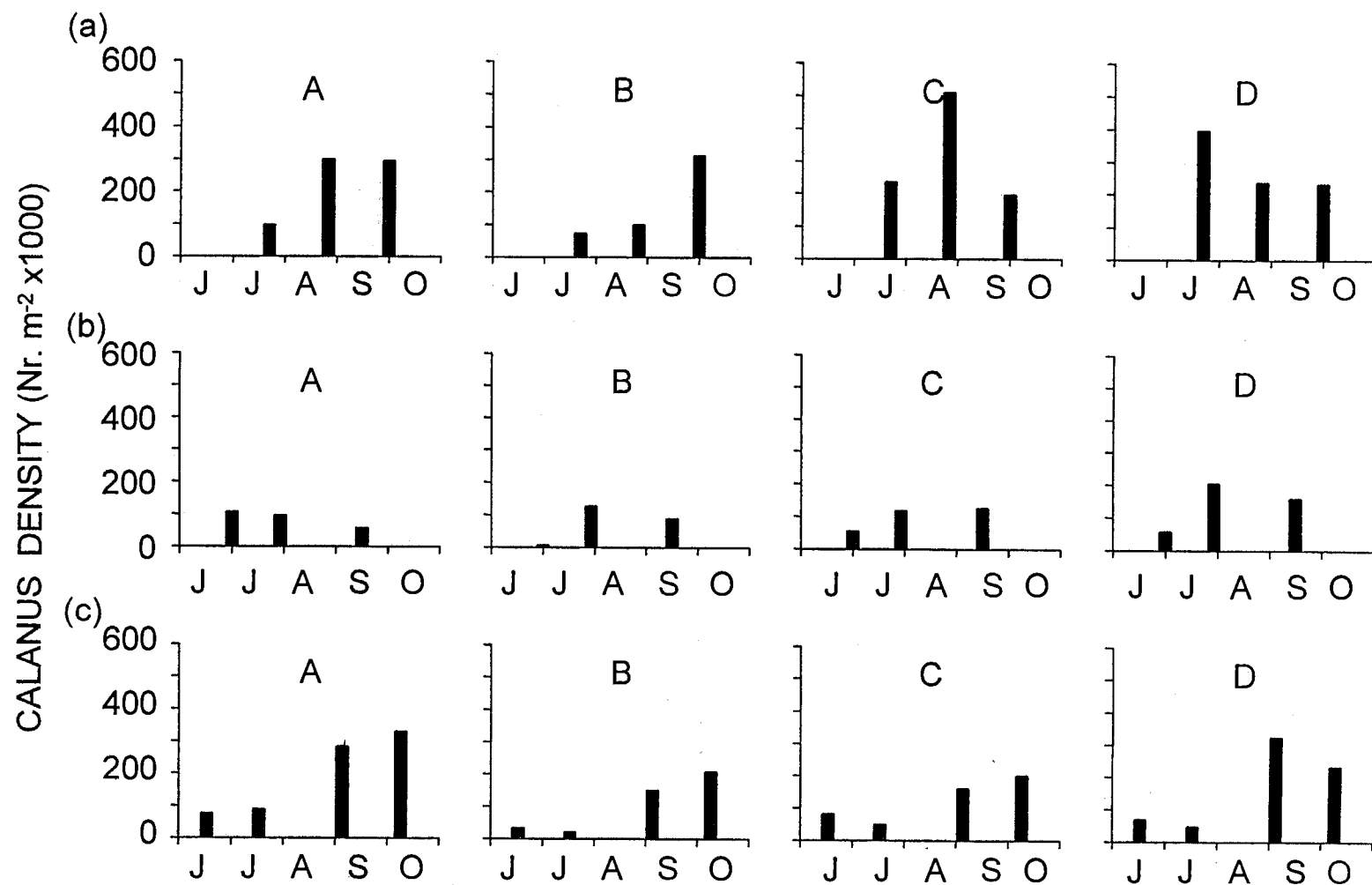
Appendix B.1. Seasonal changes in mean body length of cyclopoids at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



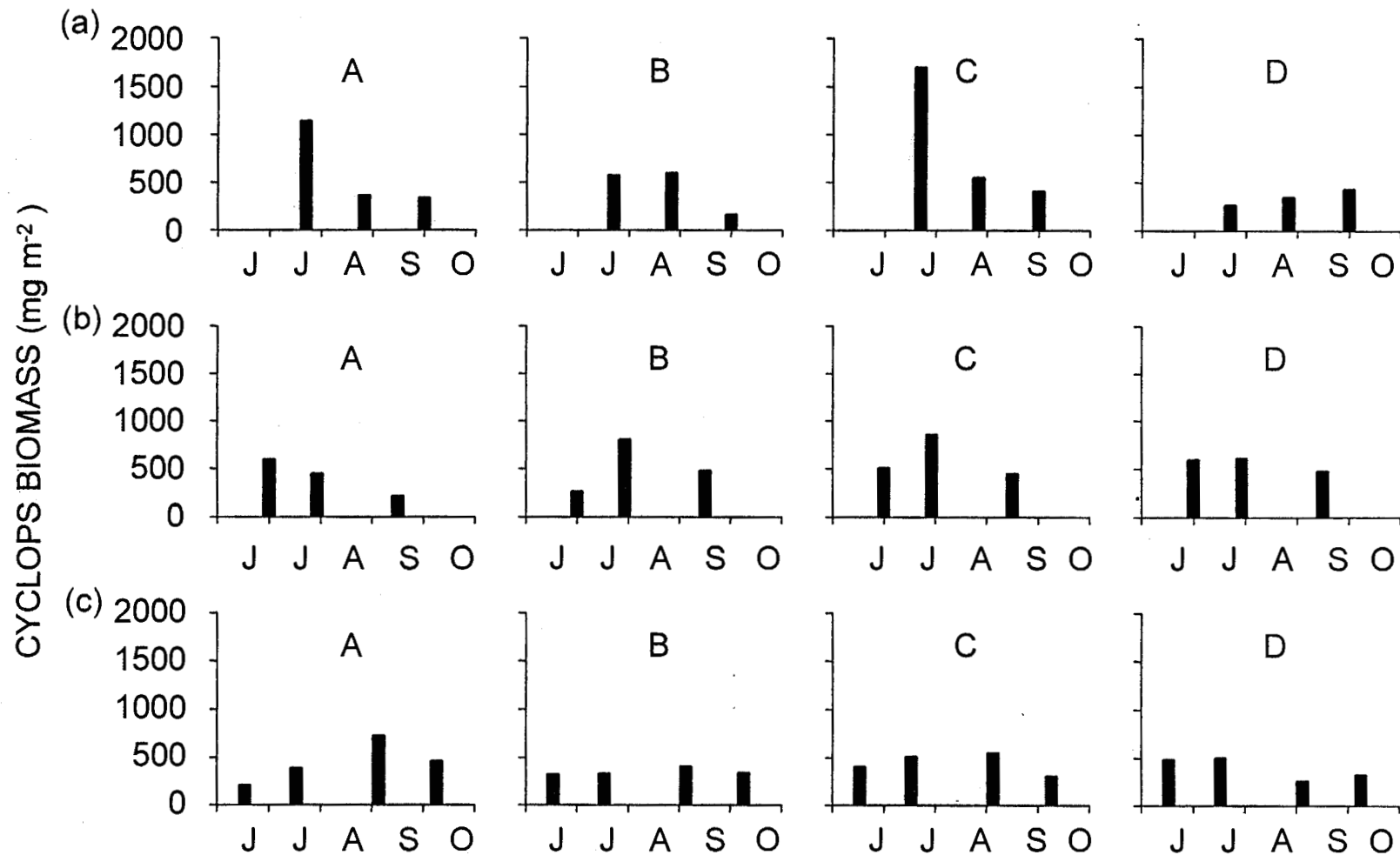
Appendix B.2. Seasonal changes in mean body length of *Diaptomus* spp. at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



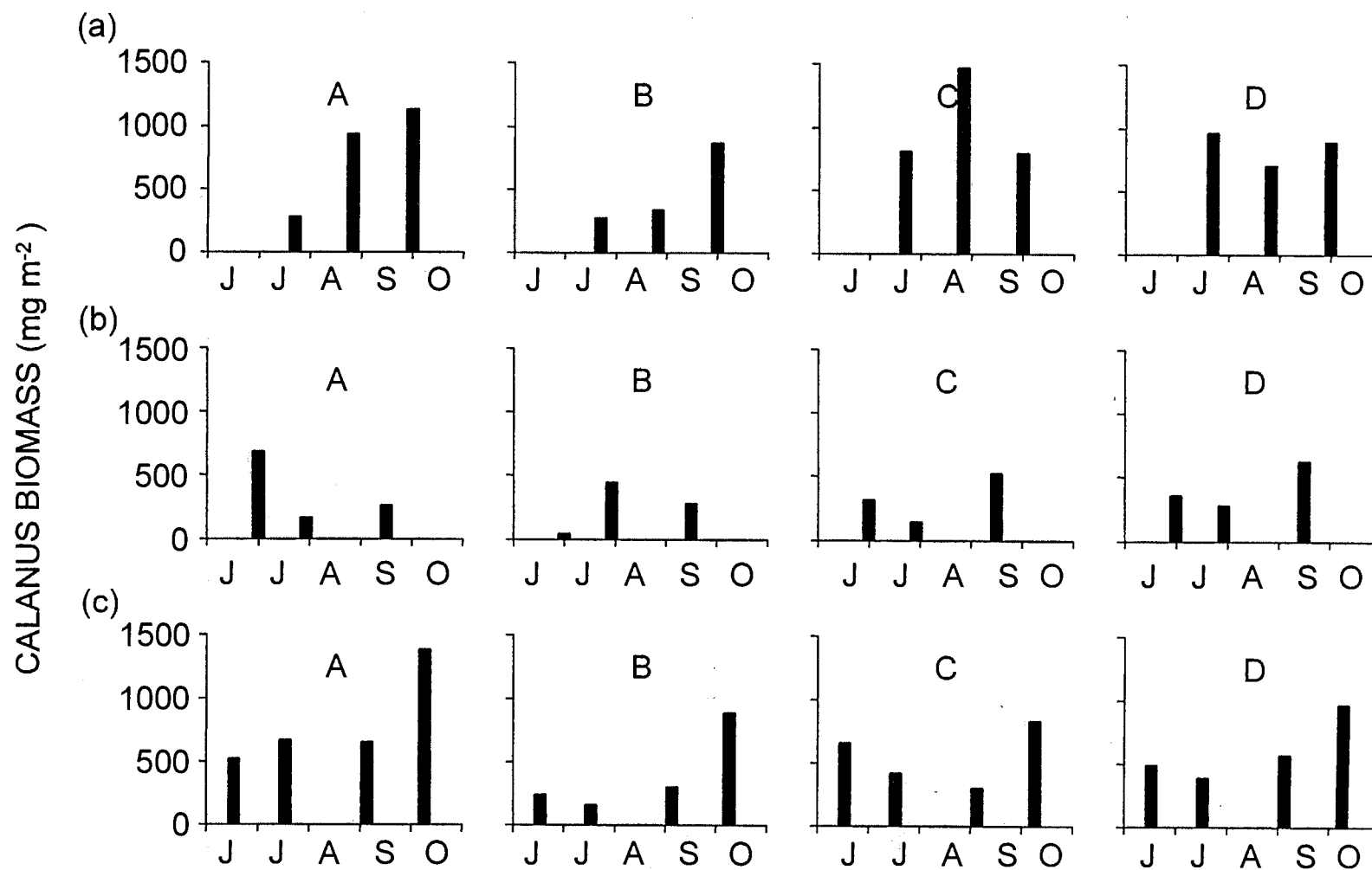
Appendix B.3. Seasonal changes in cyclopoid density at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



Appendix B.4. Seasonal changes in calanoid density at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



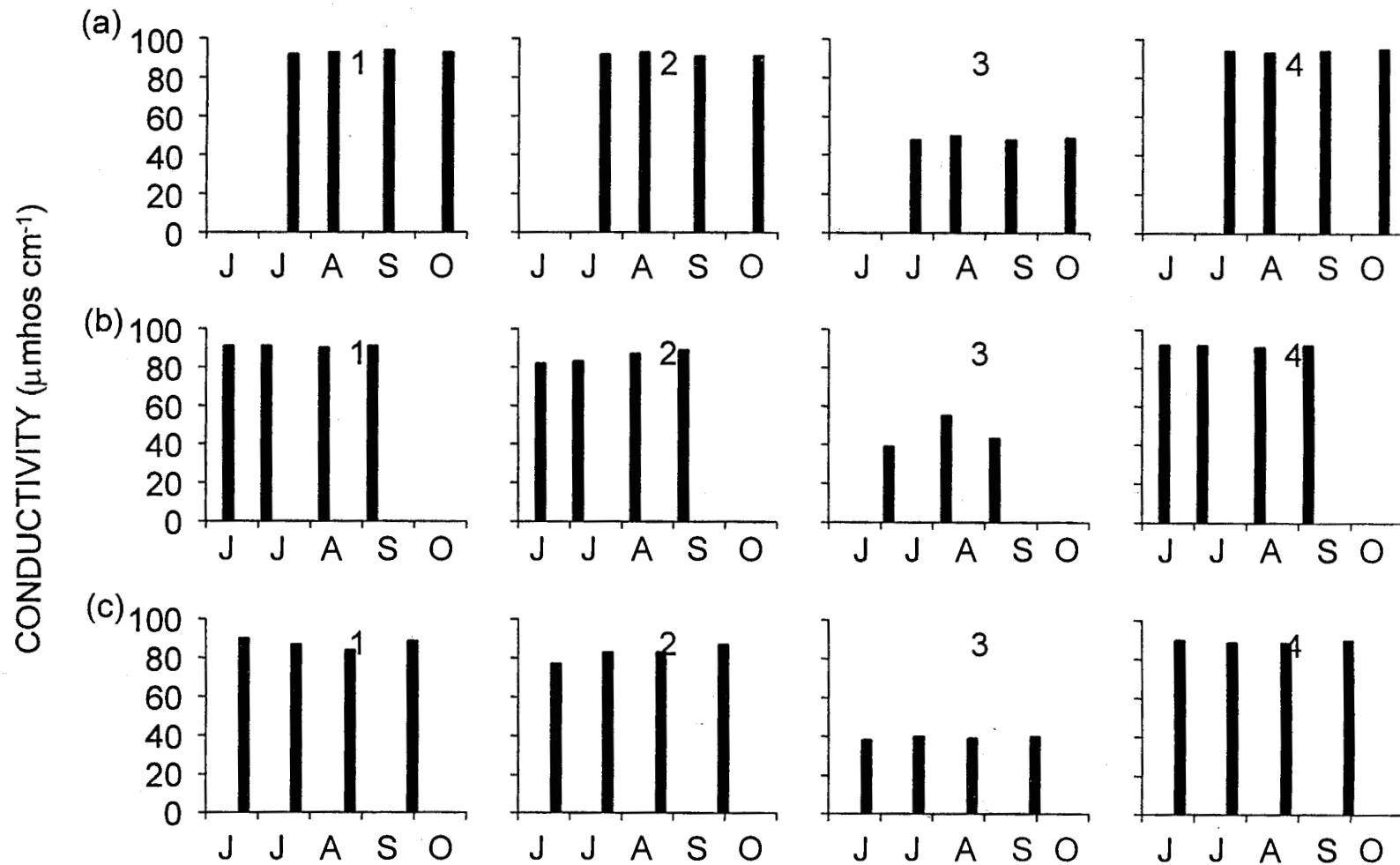
Appendix B.5. Seasonal changes in cyclopoid biomass at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



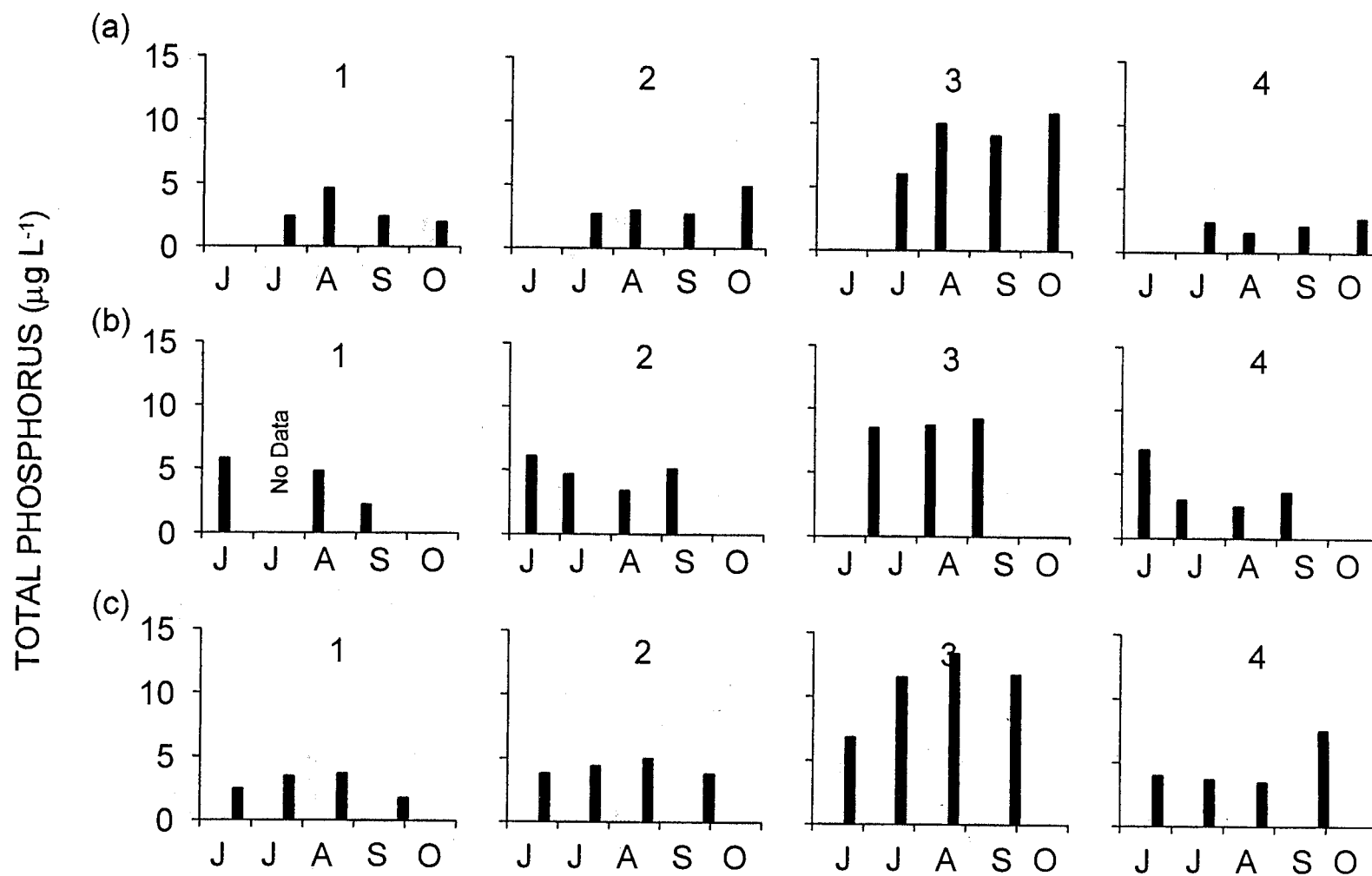
Appendix B.6. Seasonal changes in calanoid biomass at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.

APPENDIX C

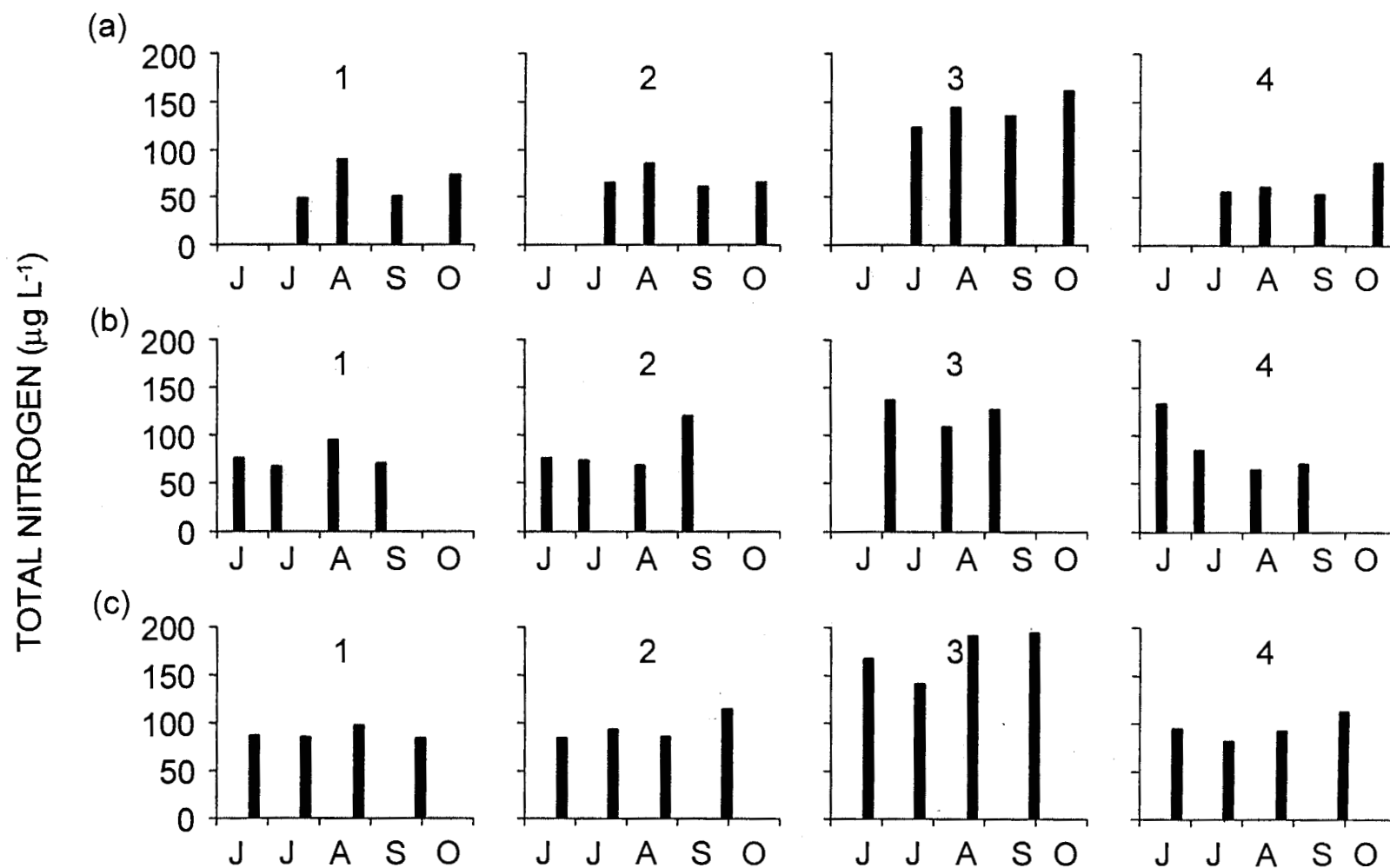
Seasonal Changes in Salient Water Chemistry, Nutrients, and Chlorophyll *a* in Becharof Lake, 1997-1999



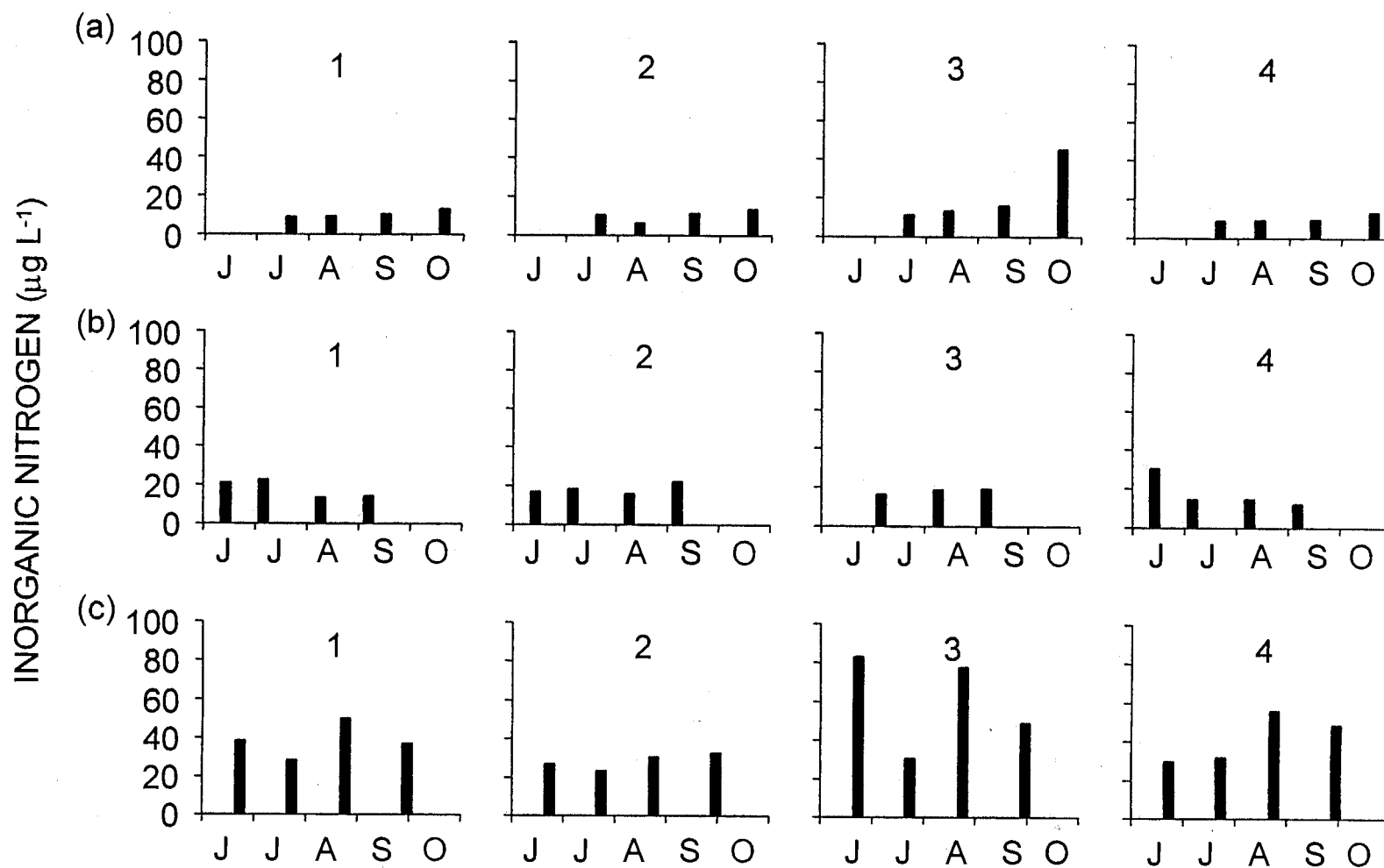
Appendix C.1. Seasonal changes in conductivity at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



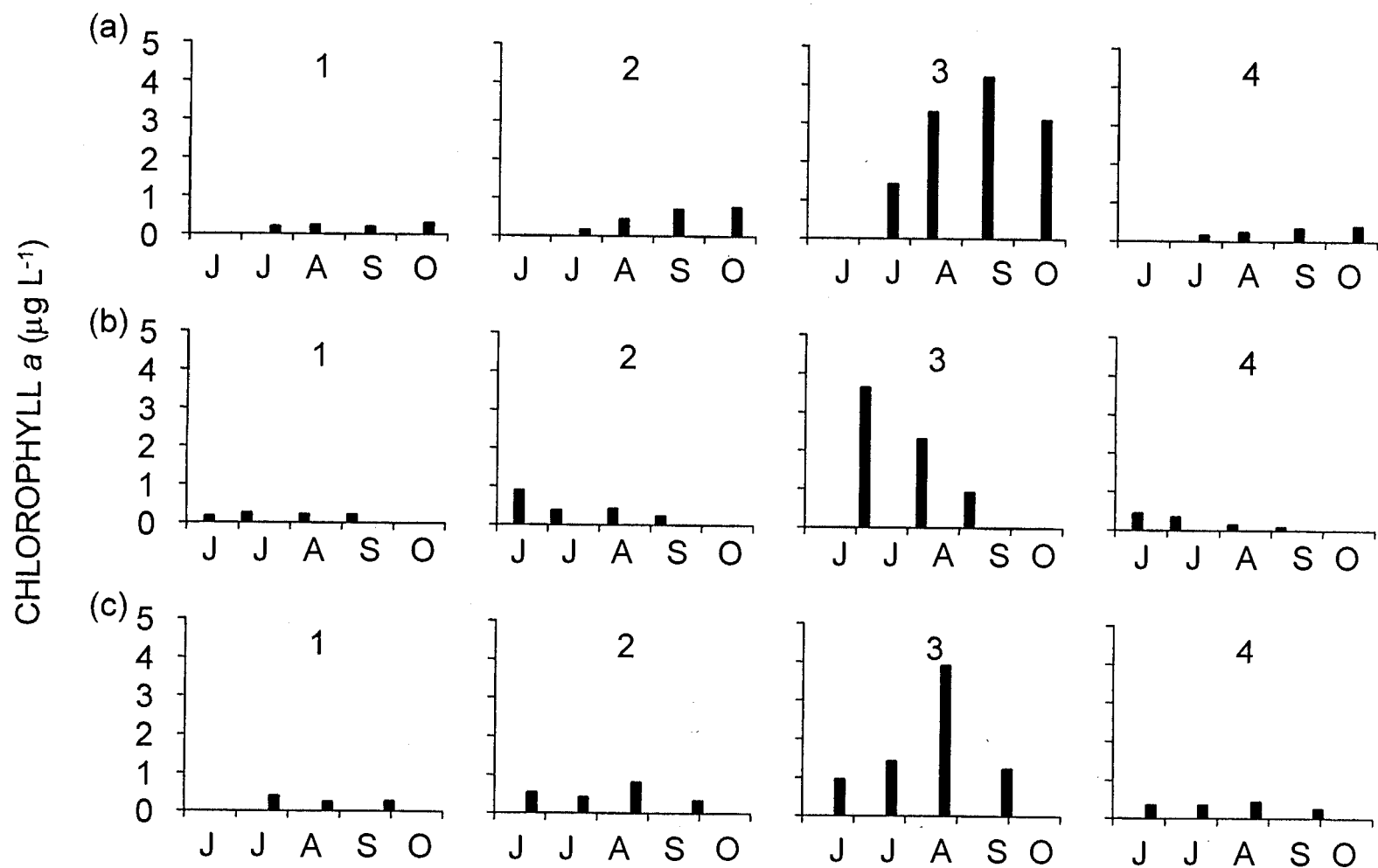
Appendix C.2. Seasonal changes in total phosphorus concentration at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



Appendix C.3. Seasonal changes in total nitrogen concentration at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



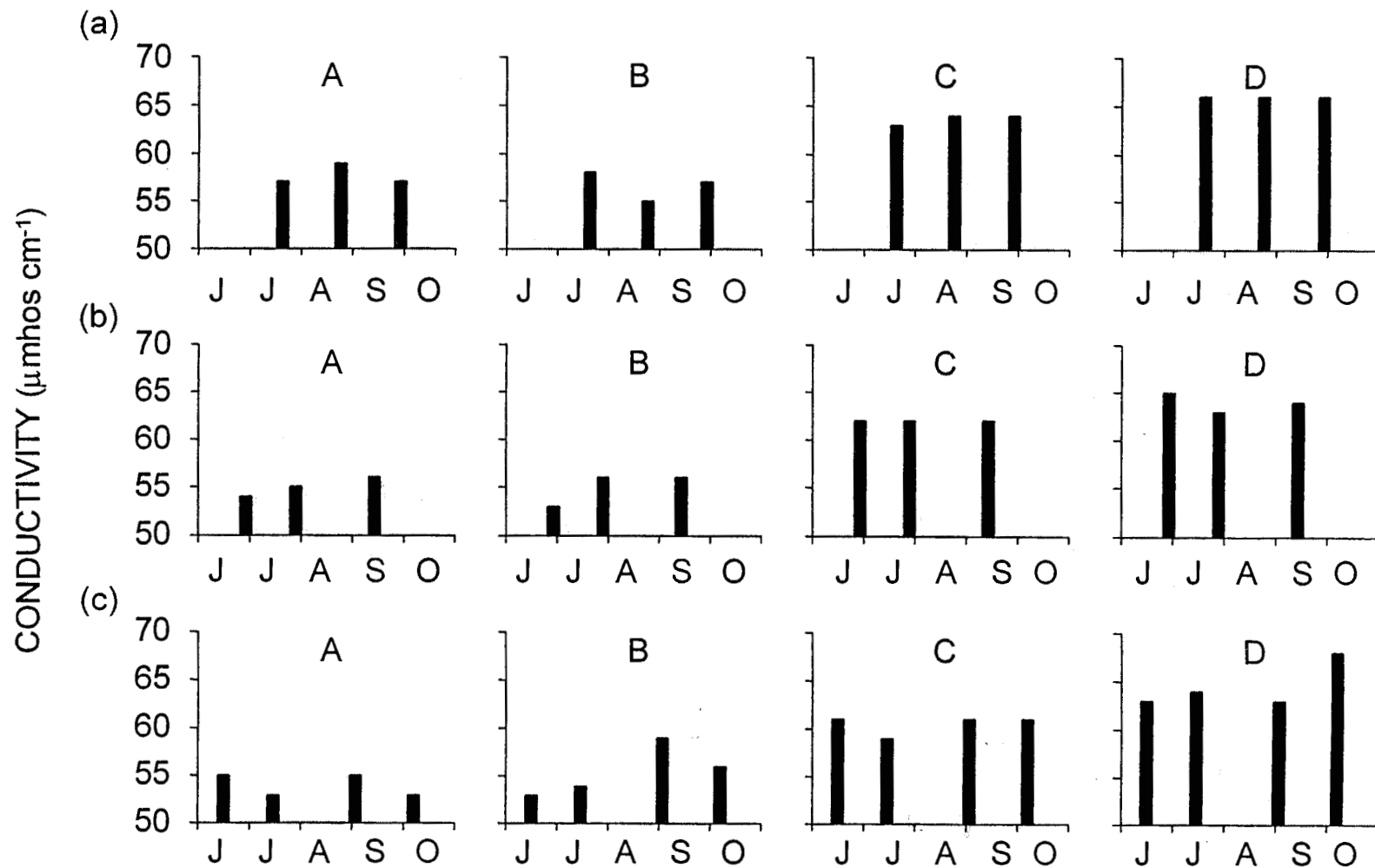
Appendix C.4. Seasonal changes in total inorganic nitrogen concentration at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.



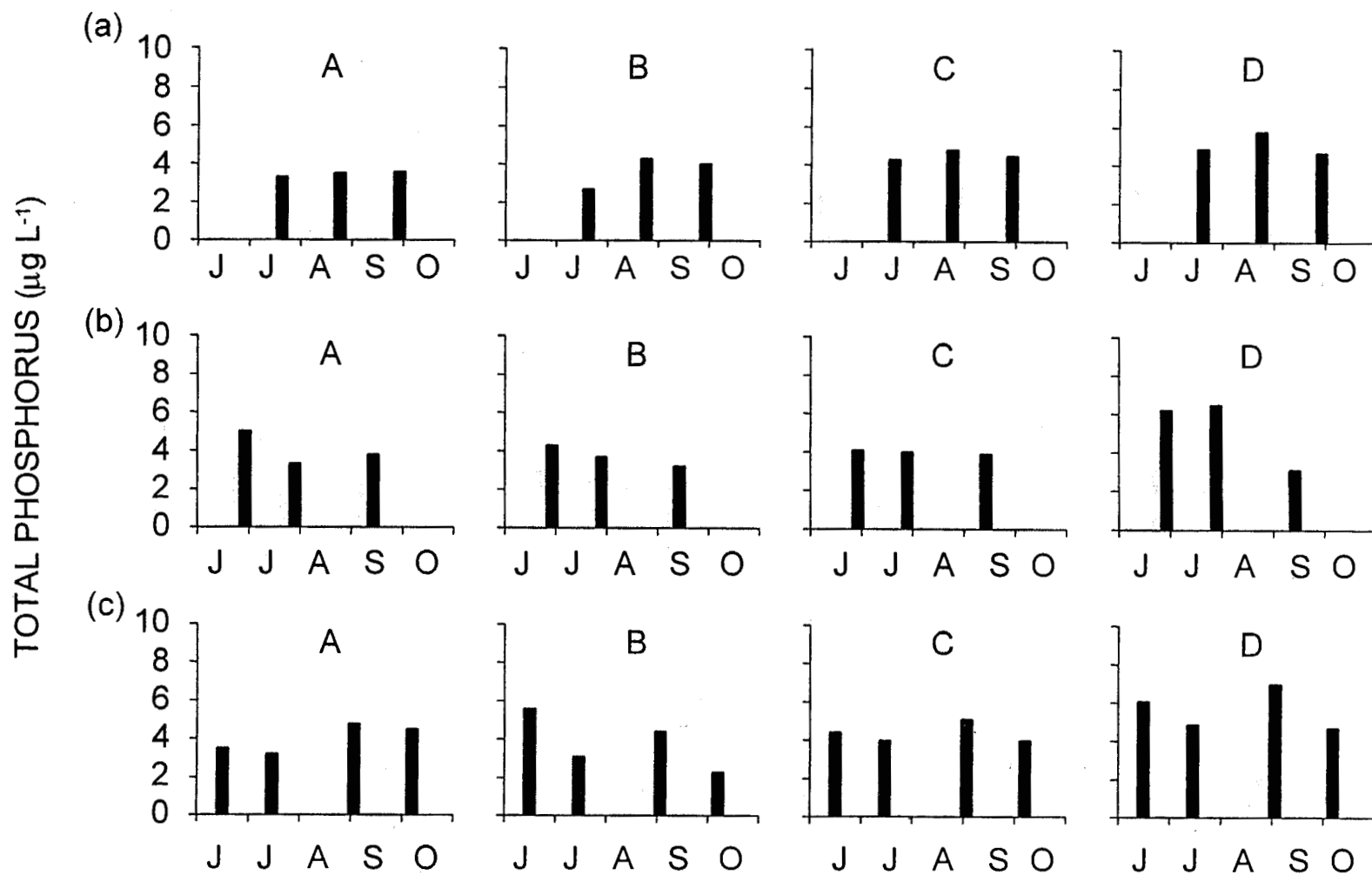
Appendix C.5. Seasonal changes in chlorophyll *a* concentration at four sites in Becharof Lake, (a) 1997, (b) 1998, and (c) 1999.

APPENDIX D

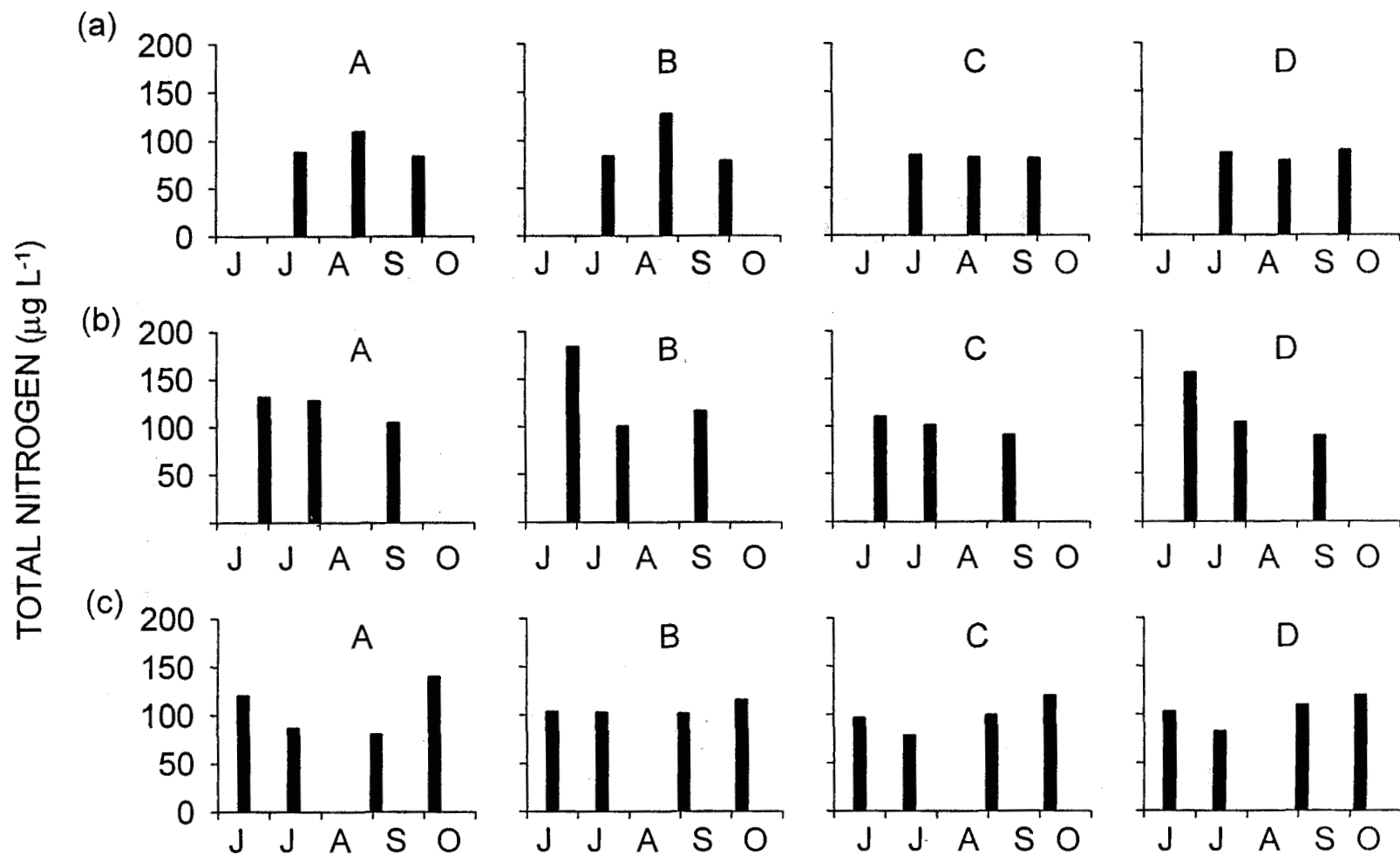
Seasonal Changes in Salient Water Chemistry, Nutrients, and Chlorophyll *a* in the Ugashik Lakes, 1997-1999



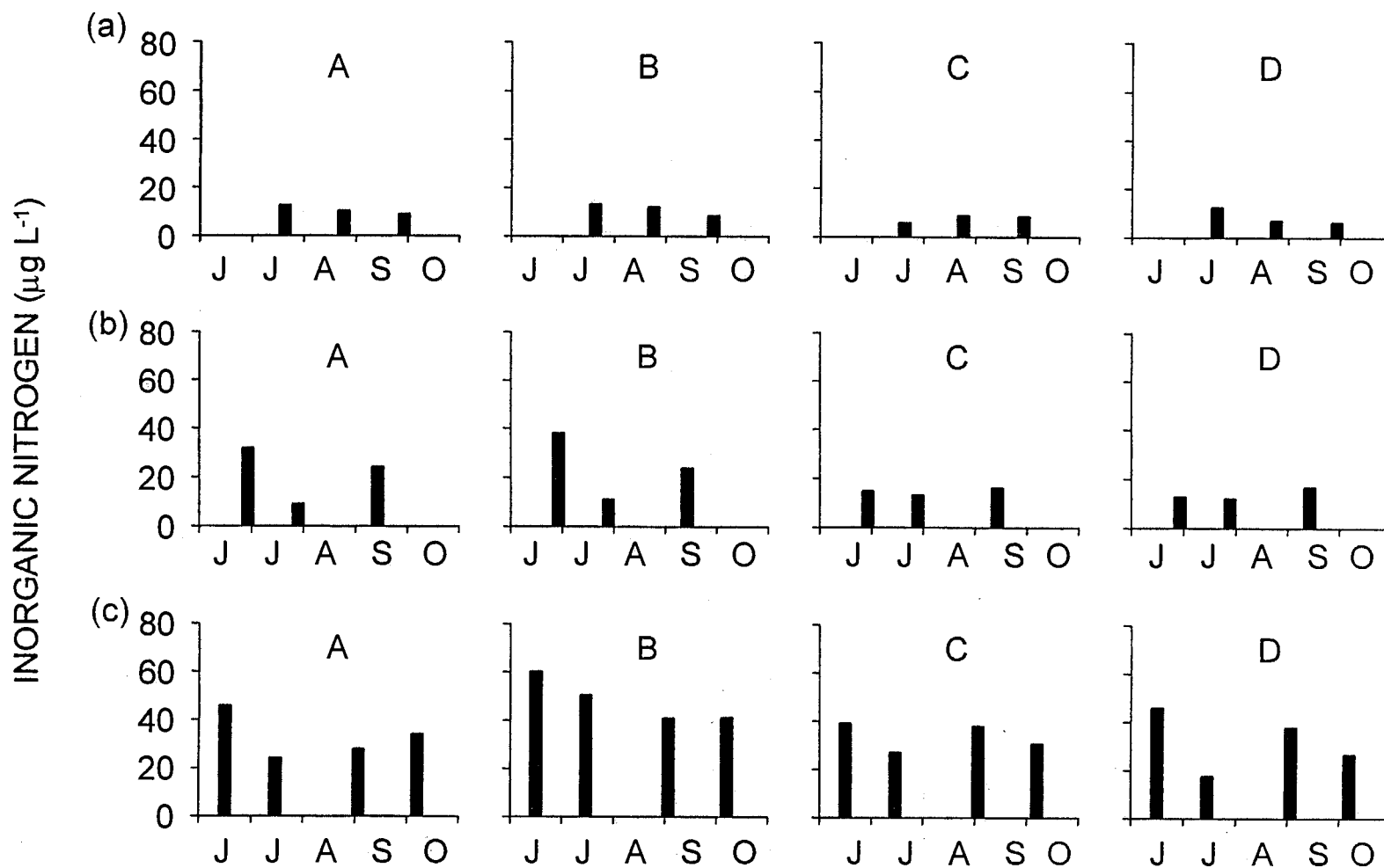
Appendix D.1. Seasonal changes in conductivity at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



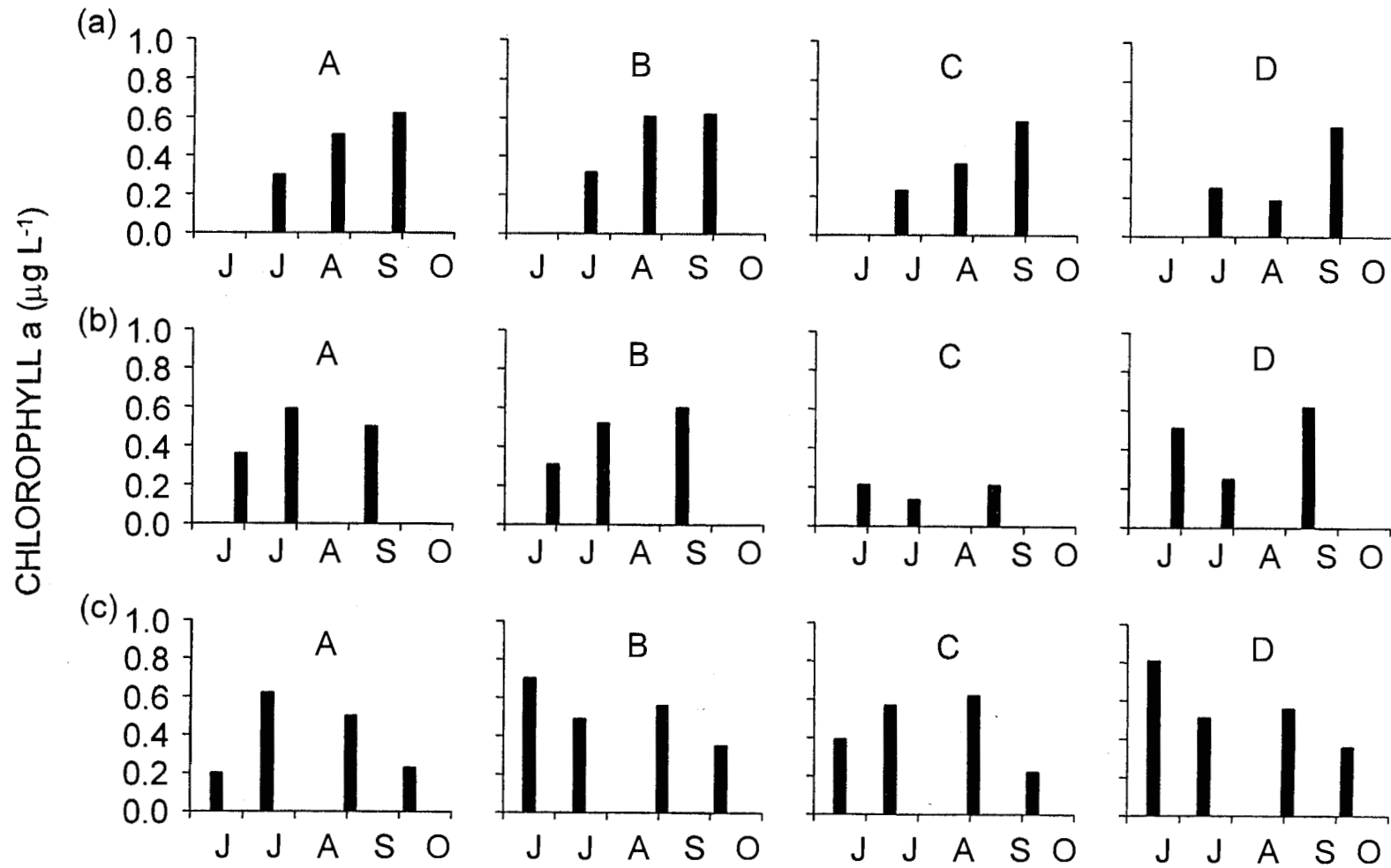
Appendix D.2. Seasonal changes in total phosphorus concentration at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



Appendix D.3. Seasonal changes in total nitrogen concentration at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



Appendix D.4. Seasonal changes in total inorganic nitrogen concentration at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.



Appendix D.5. Seasonal changes in chlorophyll *a* concentration at four sites in the Ugashik lakes, (a) 1997, (b) 1998, and (c) 1999.

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